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MORPHOLOGY OF THE HONEYBEE LARVA[1]

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INTRODUCTION

The observations here recorded seem desirable for several reasons. In the first place, it has been the policy of the Office of Beekeeping Investigations to secure, as far as possible, comprehensive and detailed information regarding all phases of the life history of the honeybee. An account of the development of the honeybee in the egg already having been completed (*36*)[2], a study of the postembryonic development appears next in order, and this involves necessarily a thorough and intimate knowledge of the structure of the larva. Moreover, an account of the structure of the bee larva ought not to be entirely without interest to intelligent beekeepers. Finally, such an account will unquestionably prove valuable to investigators of the pathology of brood diseases of the honeybee.

No complete description of the structure of the larva of the honeybee has yet been published. This is especially surprising in view of the attention bestowed on the structure of the imago. Leuckart and Nitsche (*31*) have included the bee larva in the series of types illustrated by their wall charts. These illustrations, however, convey but a meagre amount of information on this subject and in some respects are incorrect. Anglas (*1*) gives a description of the bee larva in his account of the metamorphosis of the wasp and that of the honeybee, but here again the description of the morphology of the larva is only incidental and for the most part brief and superficial. Moreover, some organ systems, such as the nervous system, are left almost untouched.

In the following account the larva has been treated as if it constituted a single stage. The larval period, it is true, embraces a series of stages, differing from one another and representing a continuous process of development, but the principal morphological features peculiar to the larva as such remain surprisingly constant. Since a sketch of the structure of the newly-hatched larva has already been published by the writer in connection with the embryonic development, and, since it is especially important to know the structural conditions immediately preceding pupation, especial attention is here paid to the larva which has virtually attained its full growth. The following descriptions therefore apply to such a larva, unless otherwise stated. Wherever important changes in larval structures accompany growth, these are taken into consideration.

EXTERNAL FORM

In general appearance the bee larva much resembles many other cruciform larvae. When removed from the cell the full-grown larva (Pl. 1, D) is fusiform, the posterior end being the larger. Younger larvae are more slender and more nearly cylindriform, while the head is much larger in proportion to the trunk. In those recently hatched the body differs in its proportions from the bodies of

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[2] Reference is made by number (italic) to "Literature cited," pp. 1208–1212.

older larvae in that the anterior end is the larger, the body tapering toward a pointed posterior end. In old larvae the posterior end is blunt and rounded. In larvae of all ages the body is strongly flexed toward the ventral side. In marked contrast the larvae of the Vespidae have bodies which are nearly straight.

In color the larva is ivory white. As seen in the comb it appears to be pure white by contrast with the brown comb, but when removed and placed on a white surface it takes on a yellowish or brownish tinge.

A series of sharply defined constrictions divides the body into 13 segments, 3 thoracic and 10 abdominal.[1] In antero-posterior extent the three thoracic segments are subequal and slightly inferior to the adjacent abdominal segments. The latter are also subequal in extent, with the exception of the 9th and 10th. The 9th is short and has a somewhat discoid form, as shown in the figure. The 10th is quite small and also discoid and bears in its center a low papilla on which is situated the anal opening.

The ventral or sternal surface is marked off from the lateral surfaces by a deep groove, the ventrolateral suture (Pl. 1, D, *VlS*), which extends from the 1st to the 8th abdominal segments, being absent on the three thoracic and the last two abdominal segments. The lateral surfaces of the abdominal segments, with the exception of the last two, are raised to form rounded lobes, the epipleural lobes (*EpL*). These lobes, while sharply marked off from the ventral surface by the ventrolateral suture, merge almost imperceptibly into the dorsolateral surfaces of the body. The epipleural lobes are often more or less confluent, producing the appearance of a beaded ridge on each side of the body. The abrupt termination of these ridges at the posterior boundary of the third thoracic segment produces the appearance of "shoulders" noted by White (*50*).

Ten pairs of spiracles are present, belonging as usual to the 2d and 3d thoracic and the first eight abdominal segments. They appear externally as minute circular apertures, each of which is surrounded by a narrow chitinous ring, the peritreme. They are located at the same level on all of the segments, about half way between the dorsal mid-line and the ventrolateral suture, and lie close to the anterior edges of their respective segments in depressions confluent with the intersegmental constrictions. In the thoracic region the first pair of spiracles has the appearance of belonging to the 1st instead of to the 2d thoracic segment, this appearance being due to the somewhat peculiar outline of the contiguous margins of these two segments (see fig. 4, A). Below the spiracles of the 2d and 3d thoracic segments the oval outlines of the wing rudiments (*WngR*) may be somewhat indistinctly seen. On all of the segments bearing spiracles a shallow linear depression or suture arises in the neighborhood of each spiracle and takes an oblique course dorsad and caudad across the dorsolateral surface of the segment toward the dorsal mid-line, where it disappears, thus separating the dorsal half of the segment into anterior (*Prs*) and posterior (*Scs*) divisions. Comparison with coleopterous larvae, such as those of Dendroctonus (*17*), makes it evident that the anterior division corresponds to the prescutum, while the posterior, which is confluent laterally with the remainder of the segment, corresponds to the scutum and scutellum together, which in the coleopterous larva are separated by a suture. These divisions, and in fact the entire contour of the body, are intimately related to the internal structure, as will be more completely explained in the description of the muscular system.

The head (Pl. 1, F, G), with regard to its general outline, may be described as bluntly conical, the base of the cone being formed by the head capsule, the apex by the labrum and the other mouth parts. The head is joined to the

[1] Embryological evidence indicates that there are actually 12 segments represented in the abdomen of the bee larva (*56*, *58*).

trunk by nearly its entire width, a sharp and narrow constriction representing the neck region. Normally the head is retracted into the prothoracic segment, thus forming a deep fold between the two. The ventral third of the head, including the labium, maxillae, and that part of the head capsule to which they are attached, is sharply separated from the remainder of the head, which constitutes the head capsule (*26*), by a deep furrow which extends on each side from between the bases of the mandibles and maxillae to the posterior limits of the head. This may be conveniently designated as the *lateral furrow*.[4] Its posterior end, on each side, is continuous with the lumen of the posterior arms of the tentorium (*2Ten*). In face view the head capsule is seen to be divided dorsally into two equal lobes by a median cleft (Pl. 1, F). On the convex surface of each of these lobes is a small rounded elevation (*Ant*), representing the distal end of the antennal rudiments. Springing from the head capsule in the mid-line, between the antennal rudiments and directed cephalad and ventrad is the cushion-shaped common rudiment of the labrum and clypeus (*Clp+Lm*). Its distal end is free from the head capsule and its tip slightly indented in the mid-line.

In Vespa, according to Kirmayer (*26*), the labrum is distinguishable from the clypeus, but apparently this is not always possible, since the two areas are represented as distinct in Kirmayer's figure 30, but not in his figures 28 and 29. In the bee larva they are not always readily distinguishable on the exterior, but in many preparations of the head of advanced larvæ the rudiment of the clypeus and labrum is seen to be crossed by a delicate and distinct fold, dividing it into a distal and a proximal part, which can only be labrum and clypeus, respectively (Pl. 1, F). These two parts are also evidently indicated by the arrangements of the muscles. (Pl. 6, C.)

Beneath the labrum is the mouth opening (*Mth*), on each side of which are the conical mandibles (*Md*), curved in such a way that their pointed tips lie beneath the labrum. The maxillæ (*Mx*), which are attached to the ventral part of the head capsule, are situated somewhat farther apart than the mandibles. They are also longer and of larger diameter, converging a trifle toward the mid-line, cylindrical in form, slightly tapering toward their apices, which are rounded and tipped each with a small spine. The labium (*Lb*), which springs from the ventral part of the head in the mid-line, is of relatively large size, projecting beyond the other mouth parts, bluntly conical in form, rounded at the apex, on which is a transversely elongated elevation bearing the slit-like common opening of the silk glands (*SlkDO*). On each side of the latter, and slightly ventrad to it, is a small spine, similar to those on the maxillæ. The upper surface of the labium is separated from the lower surface of the labrum by a narrow cleft, forming the mouth opening (*Mth*) which is bounded laterally by the mandibles and maxillæ. All of the mouth parts are soft and fleshy and covered only by thin chitin, with, of course, the exception of the small spines already mentioned.

Above the common rudiment of the clypeus and labrum, on each side of the mid-line, a shallow depression is found. These depressions represent the insertions of muscles on the inner surface of the head capsule. Above each of the antennal rudiments is a smaller but somewhat more sharply marked triangular depression; these also mark points where muscles are inserted.

[4] A study of the figure by Kirmayer (*26*) of the head of the wasp at different stages makes it evident that the "lateral furrow" of the wasp larva corresponds very closely with the margins of the fossa of the proboscis in the imago and this of course must be also true in the honeybee. It would appear, therefore, that the ventral part of the larval head lying between the two lateral furrows becomes later differentiated into the various structures included in the fossa of the proboscis—mentum, submentum, cardines, etc., and also that part of the occipital region ventrad to the foramen.

The description above given applies to a bee larva four or five days old, after removal from the cell. The larva is never permitted to assume this form, however, until after the cell is sealed, when it undergoes the important changes preliminary to pupation. The actual shape assumed by the bee larva of from four to five days old is shown in Plate 1, E. The specimen from which this drawing was made was fixed and hardened in the normal position in the cell, from which it was afterwards extracted. As can readily be seen, the larva is bent ventrad in the shape of the letter U, head and anus being brought close together, and fits its narrow quarters so completely and so snugly that it forms a veritable cast of the interior of the cell, the prismatic six-sided form of the latter being plainly reproduced by the larva, which not only takes nourishment and grows in this compressed state, but on being withdrawn from the cell can immediately assume the plump, rounded form shown in figure 1, the only remaining perceptible evidence of its close confinement being a slight asymmetry of the 8th abdominal segment, the lateral fold on this segment being more turgid on the side turned toward the bottom of the cell. This is evident in Plate 1, E. In all the specimens of larvæ fixed and hardened within the cell the head lies somewhat closer to the mouth of the cell than the anus, the long axis of the larva thus being spirally curved. In some larvæ the right side is outermost, in others the left.

Kellogg (*24*) has given a brief account, accompanied by two figures, of the head and mouth parts of the honeybee in connection with a study of the metamorphosis. It is of interest to note here that the spines on the maxillæ were found to represent the minute one-segmented maxillary palpi of the adult. This may readily be seen in stained and cleared preparations of the head of larvæ about to pupate. Kirmayer (*26*) has given a detailed account of the structure of the head of Vespa in connection with the changes taking place during the metamorphosis. Kirmayer's excellent figures of the head of the larva of Vespa show that while it is similar to that of the honeybee, it differs much in details, and particularly in the proportions of the various parts. It may be noted that in general the head of the larva of Vespa is both shorter and narrower than that of the bee larva, the labrum being indented ventrad and even a trifle caudad. (Pl. 10, A.) The labium is relatively much smaller, while the head capsule lacks the conspicuous median dorsal cleft seen in the honeybee.

HYPODERMIS AND CUTICLE

The hypodermis, which, together with the cuticle secreted by it constitutes the body wall, is a simple one-layered epithelium, differing in thickness in different parts of the larva. These differences are indicated in many of the illustrations, but it may be said that in general both hypodermis and cuticle are thin over the entire extent of the trunk, the hypodermis being as a rule thinner at the middle of the segments and increasing in thickness in the intersegmented regions, and therefore ranging from the squamous to the cuboidal type. In the head the hypodermis has a considerably greater average thickness than in the trunk (Pl. 2, B, and 3, D). The hypodermal cells here have as a rule a prismatic form, and are in many places so slender and so closely crowded together that the nuclei are compelled to lie at different levels, giving the impression of a many-layered epithelium. It should be noted that in the larva there is no thinning of the hypodermis or cuticle at the borders of the segments or at the bases of the mouth parts. Such a thinning would correspond to the articular membranes of the imago.

The rudiments of the antennæ, wings, legs, and genitalia remain to be mentioned, since they are hypodermal structures. The antennal rudiments of old larvæ are ovoid in form and are situated in deep depressions or cavities (peripodal

cavities) on either side of the labrum. They are directed cephalad and slightly mesiad, their smaller ends directed outward, and are attached by the mesial side of their larger inner ends to the head capsule on the mesial side of the peripodal cavities. The long axis of the rudiments is therefore actually bent through an angle of about 90 degrees (Pl. 2, D). The cavities themselves are closed only by the chitinous cuticle, which is continuous over their external openings. The tips of the antennal rudiments project slightly above the general surface of the head and produce the small rounded elevations visible from the exterior (Pl. 1, F and G, *Ant*). The segments of the antennæ are indicated by the wavy contour of their hypodermis as well as by the distribution of the antennal nerve. (Pl. 2, D, *AntNv*.)

The leg rudiments (fig. 1 and 4, A, *1L–3L*) are short fusiform or ovoid in shape, like the antennæ, and are also situated in deep open depressions covered externally only by the cuticle. The leg rudiments are directed caudad and mesiad. The segments of the imaginal legs are indicated by annular constrictions. The wing rudiments are flat hollow outgrowths of the hypodermis of the mesothoracic and metathoracic segments and are situated in shallow depressions low down on these segments, close to the ventral surface and at a considerable distance ventrad to the stigmata of these segments (fig. 1, Pl. 1, D, and fig. 4, A, *WngR*). In outline the wing rudiments are heart-shaped.

The rudiments of the genitalia (fig. 1, *1G–3G*) are six in number, one pair being situated on the sternite of the 8th abdominal segment and two pairs on the 9th abdominal segment, as described by Dewitz (*9*). At this stage they are small knob-like outgrowths situated in open depressions.

While the cuticle of the trunk is thin and elastic, that covering the cranium is much thicker and forms a more or less rigid capsule for the protection of the contained brain and other organs. The chitin covering the mouth parts is, as has already been said, thin and relatively flexible.

The rigidity of the head capsule is further increased by the cranial endoskeleton or tentorium, formed during the embryonic period by invaginations of the ectoderm (*36*). In the imagoes of insects the tentorium is evident as a framework of chitinous bars, but in the bee larva the embryonic conditions persist so that the tentorium consists of tubular ingrowths of the hypodermis lined with chitin, the hypodermal portion being relatively well developed as compared with the imago, in which the hypodermis forms a relatively insignificant layer. Lying between the oesophagus and the suboesophageal ganglion, transverse to the long axis, is a wide tube lined with a thick layer of chitin, compressed in a dorsoventral direction and slightly curved, the convex side being directed cephalad. This tube is subdivided—on embryological evidence—into three nearly equal parts, a central body (Pl. 1, A, and 6, D, *Ten*), and two lateral arms, the "posterior" arms (*2Ten*). The latter become continuous with the walls of the head capsule at the posterior ends of the deep lateral furrows of the head. These infoldings, or at least their posterior part, may in fact be considered as the expanded distal ends of the posterior arms, the furrows leading at their posterior ends directly into the lumen of the posterior arms, which, together with the lumen of the central body, forms a continuous open passageway from one side of the head to the other. At the junction of the central body with the lateral arms arise the anterior arms (Pl. 1, A, *1Ten*) which extend cephalad and dorsad to the anterior wall of the head capsule, with which they are united. These points of junction are marked on the exterior by two minute pits, situated above the bases of the mandible at the sides of the labrum (Pl. 1, F, *1Ten*). The anterior arms are also tubular but are much more slender than the posterior arms and are round in section. Halfway between their anterior and posterior ends each of the anterior arms gives off a

slender spur dorsad and laterad. These serve as the tendonous insertions of short muscles inserted on the anterior wall of the cranial capsule.

The mandibular apodemes also claim attention here. These are slender tapering chitinous spines which arise from the base of each mandible on its mesial side and are directed caudad and dorsad (Pl. 1, A, *RAp*). These, as their name indicates, serve as tendonous insertions for the large adductors of the mandibles. These spines are hollow for a considerable part of their length and are both accompanied and produced by corresponding involutions of the hypodermis.

White (*50*) has already called attention to the minute spines of the larval cuticle. These are more or less irregularly scattered over the surface of the cuticle of the head and trunk, the distance between them varying from 5 to 30 microns. Their length does not exceed the thickness of the cuticle, which is 5 to 6 microns. On the mesial surface of the tips of the maxillae these spines are however quite numerous, while the extreme tip of the labrum is clothed with thick-set chitinous spines, longer and more slender than those found elsewhere.

The head capsule and endoskeleton of the head of the bee are, except for slight differences in proportion, identical with those of the larva of Vespa, as described by Kirmayer (*26*).

NERVOUS SYSTEM

The general features of the nervous system of the bee larva have already been described in an earlier publication (*36*). These features indicate on the whole a conformity to the simple type found in many insect larvae. In the bee larva this simple type persists throughout larval existence, although histological changes are continually taking place, especially in the brain, in the direction of the imaginal condition. In comparison with certain other insect larvae, such as Corydalis (*13*), the nervous system of the bee seems deficient, particularly with regard to the sympathetic nervous system. This may, however, only argue a deficiency in observation. The small size of the bee larva and the abundance of fat tissue, which more or less completely fills all the spaces of the body cavity, clinging tenaciously to whatever organs lie adjacent, constitute no small obstacle to successful dissectio n, while the tracing of nerves in sections has not been found satisfactory.

The nervous system of the bee larva has never been described or illustrated in detail. Probably the only figures worth mentioning are those of Brandt (*5*), and the one shown in the Leuckart and Nitsche wall charts (*31*), a figure widely copied in text books and evidently borrowed from Brandt. These show little more than the general plan of the nervous system, the shape and proportions of the brain and circumoesophageal connections being incorrectly represented. Brandt's figure shows correctly the number and relative size of the ganglia in the ventral chain, and also the paired connections and lateral nerves.

In describing the nervous system it may be conveniently divided into the brain, the ventral nerve cord, and the stomatogastric nervous system. The following description, unless otherwise stated, is to be understood as applying to the mature, or nearly mature, larva.

BRAIN

The brain is of relatively large size, almost completely filling the upper part of th e head capsule (fig. 1, *Br;* Pl. 1, B, C). It is divided symmetrically into two expanded crescentic halves united on their convex borders by the supra-oesophageal commissure (Pl. 1, B, *Sup Com*). Seen in face view, each half presents a mesial pyriform division, the slender inferior ends of which form the crura cerebri (*CCer*) connecting the brain with the suboesophageal ganglion (*SoeGng*); above these follow in order the small but prominent tritocerebrum (*3Br*), the

deutocerebrum, olfactory or antennal lobes (*AntL*), and the large protocerebral lobes (*1Br*). Laterad and caudad the protocerebral lobes merge into the broad auriculate optic lobes (*OpL*), which lie almost precisely in the transverse plane. Their edges are quite thin and their posterior faces almost perfectly flat. The two lobes of the tritocerebrum are recognizable externally as distinct swellings most evident in profile view (Pl. 1, C, 3Br); those of the deutocerebrum, however, are to be identified externally only by the antennal nerves which spring from them. On the anterior faces of each of the optic lobes, near their ventral margins, and involving also the antennal lobes, is a well-marked depression, of a somewhat hemispherical outline. These depressions are produced by the peripodal cavities of the antennal rudiments, which in mature larvae are of large size.

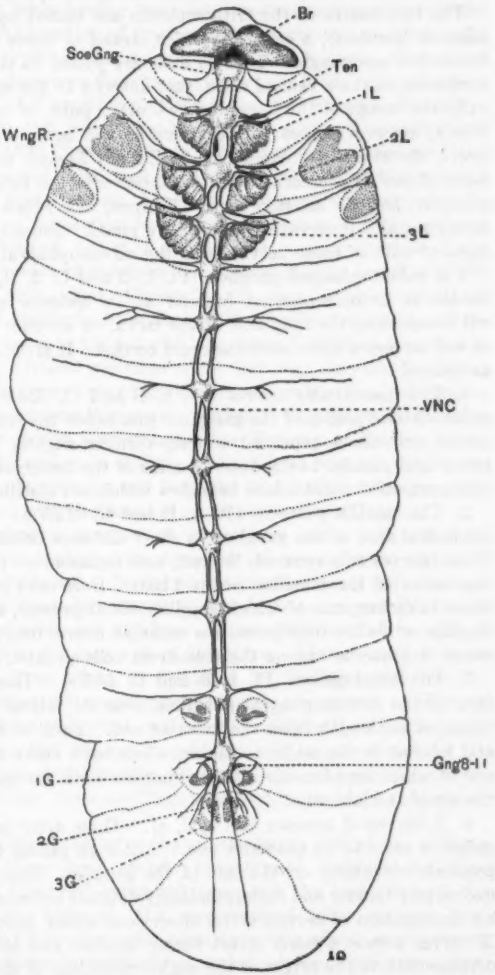

FIG. 1.—Nervous system and ventral body wall of mature honeybee larva, drawn from a dissection. ×16

Two pairs of nerve trunks arise from the brain. The first of these, the antennal nerves (Pl. 1, B and C, *AntNv*) spring from the anterolateral faces of the antennal lobes. They then take a lateral course to the base of the antennal rudiment, where each divides to form three branches. Two of these branches innervate the adjacent masses of mesodermal cells surrounding the base of the antennal rudiment, and are therefore evidently motor nerves. The third or sensory branch enters the cavity of the antenna and passes along its lateral margin, sending off a tuft of nerve fibers to each segment. This is well illustrated by Plate 2, D, which shows the antennal rudiment in longitudinal section with the nerve (*AntNv*) giving off branches to each of the six segments seen in the section. The labrofrontal nerve (Pl. 1, B and C, and 2, B, *LmNv*) springs from the anterior face of each of the two halves of the tritocerebrum. This nerve is, as its name

indicates, a double one, and near its point of origin it divides into its component parts, the frontal nerve (Pl. 1, B and C, *FtNv*), which turns mesiad to unite with the stomatogastric or frontal ganglion (*FtGng*), and the labral nerve (*LmNv*). The latter takes a cephalad course, entering the clypeus at its extreme lateral border, and runs close under the hypodermis to the tip of the labrum, where it divides into several branches innervating the hypodermis.

The two halves of the tritocerebrum are united by the suboesophageal commissure (*SoeCom*), a relatively thick strand of nerve tissue which forms a loop below the oesophagus. Its two ends are joined to the two halves of the tritocerebrum on their ventral sides, just anterior to the crura cerebri.

In the imago of the honeybee two other pairs of nerves have been described which, however, appear to be absent in the larva. These are the tritocerebral nerve, discovered by Janet (*19*) in the ant Lasius, which issues from the inner faces of the tritocerebral lobes and innervates the inferior dilator muscles of the pharynx, and the salivary nerve (Kenyon, *25*), which also issues from the tritocerebrum and innervates the salivary gland. Jonescu (*21*) has shown that the roots of both of these nerves lie in the suboesophageal ganglion.

The suboesophageal ganglion (Pl. 1, B and C, 2, B, and 3, A, *SoeGng*) is lenticular in form, somewhat broader at its anterior end, and turned obliquely with respect to the long axis of the larva, its anterior end being directed dorsad as well as cephalad to meet the crura cerebri. It gives rise to four pairs of nerves, as follows:

1. The mandibular nerves (Pl. 1, B and C, *MdNv*). These arise from the antero-lateral angles of the ganglion, just below the crura cerebri. Each of these nerves pursues a cephalad course, turning slightly dorsad and laterad, just below and parallel to the anterior arms of the tentorium, to the base of the mandible, where it divides into branches which are distributed to this appendage.

2. The maxillary nerves (Pl. 1, B and C, *MxNv*). These arise from the ventro-lateral face of the ganglion, a short distance behind the mandibular nerves. These nerves run ventrad, laterad, and cephalad to the anterior surface of the depressors of the maxillae (see p. 1190). Here each of these nerves divides into three branches, one of which supplies the depressor, a second the flexor of the maxilla, while the third pursues a cephalad course into the interior of the maxilla, where it branches among the mesoderm cells situated there.

3. The labial nerves (Pl. 1, B and C, *LbNv*). These arise from the ventral face of the suboesophageal ganglion, near its lateral borders, and about two-thirds of its length from the anterior end. Each of these nerves runs ventrad and laterad to the major retractor, where each nerve divides into two branches, one of which supplies the retractor muscle while the other continues cephalad to the tip of the labium.

4. X nerves of Jonescu (Pl. 1, C, *x*). These arise from the lateral faces of the ganglion close to its posterior end. Although taking their rise from prominent papillate elevations on the side of the ganglion, these nerves in old larvae are excessively slender and correspondingly difficult to trace. The evidence obtained by examination of several series of sections seems, however, to indicate that the X nerves pursue a fairly direct course ventrad and laterad, reaching the hypodermis close to the origin of the major retractors of the labium. In sections of recently hatched larvae these nerves are relatively much larger than in older larvae and in fact are very easily distinguished. Their course is directly laterad to the ventral margin of the junction of the posterior arms of the tentorium with the hypodermis of the neck region. No indication of a connection with the silk gland was seen. It appears therefore that in the bee larva this nerve is purely sensory. Jonescu (*21*) has described this nerve in his account of the brain of the imaginal honeybee, but is silent regarding its course and destination. The

writer has also seen it in sections of material of the imaginal bee, but has been unable to follow it to its termination. As in the larva, it is insignificant in size, although plainly evident at its point of departure from the ganglion. Janet (*18*) has described a fourth pair of nerves arising from the suboesophageal ganglion in the ant *Myrmica rubra*, and Krauss (*28*) and Hammar (*13*) have described a pair of nerves in the Corydalis larva arising from the caudo-lateral portion of the ganglion just cephalad of the junction of the connectives with the ganglion. In *Myrmica rubra* the nerve corresponding in position to the X nerve, termed by Janet "the labial sympathetic nerve (nervus sympatheticus labi)" gives rise to a complex system consisting of a ganglion and three branches on each side of the mid-line. These innervate the labial gland and also adjacent muscles and tracheae. In Melanoplus (*39*), Corydalis larva (*13*), Forficula and certain other insects (*29*) a pair of nerves make their exit from the lateral faces of the suboesophageal ganglion near its posterior end, generally known as "salivary gland" nerves. In the bee larva no connection between the X nerves and the salivary (silk) gland could be established, but it nevertheless is possible in view of the close correspondence in the point of exit from the suboesophageal ganglion of the salivary gland nerves in Melanoplus, Corydalis, etc., the labial sympathetic nerves in Lasius, and the X nerves in Apis, that these are all homologous. Pietschker (*42*) has described a nerve in the ant which he terms "nervus accessorius." It springs from the suboesophageal ganglion about half way between the labial nerve and the connectives and runs toward the labium, where it ends in depressions of the hypodermis, possibly representing sense organs. This nerve in its point of exit and its termination closely approximates the X nerve of the bee larva. The accessory nerve of Pietschker is entirely distinct from the salivary nerve which was also observed and makes its exit from the dorsal side of the ganglion. It is also not to be identified with the labial sympathetic nerve of Janet.

The brain and suboesophageal ganglion of the mature larva, with reference to their external form, differ slightly from those of the young larva, and very materially from those of the imago. In the newly hatched larva (*36*) the two lobes of the protocerebrum (including the optic lobes), as compared with those of the mature larva, are shorter and thicker, and are bent caudad instead of lying in a plane transverse to the long axis of the larva. Moreover, they show clearly a subdivision into three lobes, as described by Viallanes (*49*) for Orthoptera. The antennal lobes, although not prominent, are present as distinct swellings, while the tritocerebral lobes are scarcely differentiated externally from the antennal lobes on the one hand and the thick crura cerebri on the other. The latter merge caudad into the elongate suboesophageal ganglion, which is divided externally into three swellings representing its three component pairs of ganglia.

As compared with the brain of the larva that of the imago (*21*) shows striking differences. Superficially there is a certain resemblance between the two, principally on account of their flat expanded form and the large size of the optic lobes. In the imago, however, the protocerebral lobes become high bilobed elevations separated from the optic lobes by well marked constrictions, and the antennal lobes become conspicuous rounded swellings projecting from the anterior face of the brain; while the tritocerebral lobes, which are fairly distinct in the larva, become almost indistinguishable. Moreover, in the imago the suboesophageal commissure becomes so fused with the suboesophageal ganglion as to be indistinguishable externally, while the frontal ganglion sinks to insignificant proportions. On the other hand, the suboesophageal ganglion of the mature larva differs but little in form, size and general external appearance from that of the imago. It is scarcely necessary to remark that most of these differences, such as the difference in size of the antennal lobes, may readily be

correlated with the differences in the environmental conditions of the two forms, yet some of these differences, such as the reduction in size and relative importance of the tritocerebrum and of the suboesophageal commissure, represent developments in the direction of specialization. In other words, notwithstanding its relatively specialized form, the brain of the larva is appreciably nearer the primitive type, as represented in the lower orders of insects, than is that of the imago.

VENTRAL NERVE CORD

The ventral cord consists of 11 ganglia united by rather widely separated connectives (fig. 1, *VNC*). All of these ganglia, with the exception of the eleventh, or terminal ganglion, are situated in the anterior half of their respective segments. In form the ganglia are more or less lenticular, the first three, or thoracic, being much larger than the abdominal ganglia. The latter are subequal in size, with the exception of the eleventh or terminal ganglion, which is elongate in form and much larger than the others. Unlike the other ganglia, this one is situated in the middle of its segment, the eighth abdominal. This ganglion, as usual, is compound, consisting of three ganglia and the rudiment of a fourth (*6*, *38*), representing, respectively, the neuromeres of the 8th, 9th, 10th and 11th abdominal segments.

Each thoracic ganglion gives off two pairs of lateral nerves (fig. 1 and 4, A). The first pair arises from the antero-lateral margin of the ganglion close to the point where the latter joins the connectives. In the prothorax these nerves run laterad in the anterior half of the segment, close to the hypodermis. In the mesothorax and metathorax these nerves also run laterad, giving off a branch to the ventral trunk muscles, and, continuing onward, skirt the anterior margin of the wing rudiments. At the antero-lateral border of the latter each of these again bifurcates, one branch going to the wing rudiment while the other passes dorsad and laterad to the viscera.

The second of the two pairs of nerves given off arises from the lateral margin of the ganglion about midway of its length. The course and distribution of these nerves is the same in all three thoracic segments. Each passes laterad and slightly caudad to the leg rudiment (*1L–3L*) of the corresponding segment, sending a branch to the base of the rudiment. It then continues laterad and is lost to view among the muscles and fat cells.

Each of the abdominal ganglia, exclusive of the terminal ganglion, possesses but one pair of lateral nerves (fig. 1 and 4, B, *LNv*). These nerves run directly laterad, giving off branches to the ventral trunk muscles, as shown in Figure 4, B, and become lost to sight among the trunk muscles and viscera.

The 8th abdominal or terminal ganglion gives off four pairs of nerves (fig. 1). The first pair arises from the lateral margins of the ganglion near its anterior end and passes laterad to the muscles and viscera of the 8th abdominal segment. The second pair of lateral nerves originates so close behind the first pair that these two pairs can be regarded as having a common root. These two pairs of nerves go to the first pair of genital rudiments (*1G*). The third pair of lateral nerves runs caudad into the 9th abdominal segment, breaking up meanwhile into several branches, some of which supply the second pair of genital rudiments (*2G*). The fourth and last pair arises from the posterior margin of the ganglion, and these nerves run almost directly caudad to the 10th segment, where they break up into branches supplying the viscera and muscles of this segment. Three segments, the 8th, 9th, and 10th abdominal, are therefore represented in the terminal ganglion on the basis of the number and distribution of the lateral nerves. The fourth segment, the 11th abdominal, is represented by only an insignificant ganglionic rudiment, and its corresponding segment disappears about the time embryonic development is completed.

STOMATOGASTRIC NERVOUS SYSTEM

In the bee larva, so far as known, this is the sole representative of the so-called sympathetic nervous system. It consists of the frontal or stomatogastric ganglion and the nerves associated with it. The frontal ganglion is of relatively large size, in comparison with the imago, and is more or less pyriform in shape, its smaller end directed caudad (Pl. 1, B and C, and 3, A, *FtGng*). It is situated above the oesophagus and just in front of the brain. Its sole connection with the brain is made by means of the frontal commissures or nerves (*FtNv*), which are rather stout bundles of fibers arising from the two sides of the ganglion near its anterior end. From this point they run laterad and caudad to the anterior faces of the two halves of the tritocerebrum, joining there the roots of the labral nerves, as already described. From the anterior end of the frontal ganglion a small nerve is sent off, sometimes called the "frontal nerve." This term, however, is objectionable, since it is also commonly applied to the commissures connecting the frontal ganglion with the tritocerebrum. The nerve in question (Pl. 3, A, *SPhyNv*) runs cephalad along the dorsal surface of the oesophagus to the epipharynx, where it divides into several branches, some of which go to the epipharangeal muscles. Twigs are also apparently sent to the tip of the labrum. In view of its terminations, Janet (*18*) has termed the corresponding nerve in *Myrmica rubra* "nerf des muscles supérieurs du pharynx situés en avant du ganglion frontal." This descriptive term the writer for convenience ventures to abbreviate to "superior pharyngeal nerve" (*SPhyNv*). In *Myrmica rubra* there is another nerve to the posterior superior muscles of the pharynx. This nerve apparently is not represented in the bee larva. The posterior smaller end of the frontal ganglion is continued caudad as the stomatogastric or recurrent nerve (Pl. 3, A, *StgNv*). This nerve passes caudad in close contact with the dorsal wall of the oesophagus, meanwhile rapidly diminishing in caliber, to the posterior part of the head. Here it bifurcates, and a little farther caudad the two forks break up into branches too small to be successfully traced. In young larvae, and even in those as much as three days old, the two bifurcations of the recurrent nerve lead to flat discoid cell masses, closely applied to the sides of the oesophagus. These cell masses have been interpreted as the pharyngeal ganglia (*36*). In mature larvae they are no longer present, their places being taken by branches of the recurrent nerve, as stated above.

HISTOLOGY

The histology of the nervous system of the bee is too complex to be treated here in detail, but there are nevertheless certain outstanding features which deserve consideration.

The outer neurilemma or sheath consists of a layer of cells, usually single, limited on each side by a delicate but distinct membrane, and forms the outer covering layer of the brain, the various ganglia, the connectives, and at least the roots of the peripheral nerves. In both its thickness and in the form of its component cells the neurilemma differs much in character at different points. On the dorsal surface of the suboesophageal ganglion, for example (Pl. 2, B, *SoeGng*) the neurilemma (*Nlm*) often has the appearance of being only a single membrane, the two component membranes being actually brought very close together and the neurilemma cells being thin, flat, and spaced widely apart. At certain other points, in particular the posterior surface of the protocerebral lobes (Pl. 2, B, *Nlm*), the neurilemma is, on the other hand, very thick, and its cells, irregular and mesenchymatous in form, are seemingly disposed in several layers. Usually the neurilemma cells form a regular epithelial layer (Pl. 3, B and C, *Nlm*). Their cytoplasm, however, commonly presents a more or less shrunken and vacuolated

appearance, while the nuclei frequently stain very intensely with iron haematoxylin (Pl. 3, C, *Nlm*). An inner neurilemma is present as a more or less regular layer of small cells lying between the ganglion cells and the fibrous substance. It is best developed and most early seen in the brain (Pl. 2, B, *INlm*), and less so in the smaller ganglia. (Pl. 3, C, *INlm*.)

The brain and other parts of the central nervous system present in sections the usual core of nerve fibers and the cortical zone of nerve cells. (Pl. 2, A and B.) In the larval brain many of the features of the imaginal brain are plainly recognizable. This is particularly true of the broadly expanded optic lobes, which in transverse sections clearly display a division into inner, middle, and outer fibrillar masses (Pl. 2, A, *fm3*, *fm2*, *fm1*), while the cells and their fibrous processes show a distinct radial arrangement. In Plate 2, A, a layer of fibers intermingled with small cells is seen situated near the lateral faces of the optic lobes, between the latter and the hypodermis. These are evidently the developing postretinal fibers (*PrF*). They enter the optic lobes on the posterior surface of the latter, near their lateral margins, and may be traced around their lateral margins to the optic plates. The latter comprise two crescentic thickened areas of the hypodermis (ectoderm), one on each side of the head, their extent and relation to the remainder of the head capsule being indicated by Plate 2, C, *OpPl*.

The ocelli are present at this stage as hypodermal thickenings. Those for the two lateral ocelli are shown in Plate 2, A, *O*. The rudiment of the median ocellus lies farther cephalad, in the median groove (*43*).

Centrad and somewhat cephalad of the optic lobes, the rounded protocerebral lobes (Pl. 1, B, *1Br*) are seen to contain well-developed mushroom bodies, which are essentially similar to those of the imago (Pl. 2, B, *MB*). These bodies were found to be recognizable in a larva three days old. [5]

The deutocerebral or antennal lobes, although not evident externally, are distinguishable in sections by corresponding enlargements of the fibrous core (Pl. 2, A and B, *AntL*), and the relatively prominent tritocerebral lobes are similarly characterized (*3Br*).

The internal structure of the ganglia of the ventral nerve cord of the bee larva is simple, offering no striking peculiarities, and may probably be considered as fairly typical of the condition generally found in the simpler types of insect larvae. As seen in Plate 3, B, which represents a transverse section through the fifth abdominal ganglion, each ganglion is divided externally into right and left halves, representing the two members of the pair of primitive single ganglia. The outer surface of the ganglion is covered by a well-defined neurilemma (*Nlm*). Internally each lateral half consists of a central mass of nerve fibers, continuous with that of the connectives and surrounded by ganglion cells (*NvF*). These two central masses of nerve fibers are connected with one another by two parallel transverse strands of nerve fibers, the commissures (Pl. 3, B and C, *Com*). These are, as shown in Plate 3, C, situated somewhat cephalad of the middle of the ganglion. On the left side, in Plate 3, B, a strand of fibers (*LNvF*) is seen passing laterad from the central mass of fibers. On the right side the ganglion is seen to extend itself laterally into the lateral nerve of this side, in which is seen a strand of fibers (*LNvF*) corresponding to that of the opposite side. On the right side, however, the connection of the nerve fibers of the lateral nerve with the central mass is not shown in this section.

[5] The duration of the feeding period of the larva is from four and one-half to five and one-half days. Larvae taken at or near the end of this period are considered mature, and it is to such larvae that the description above applies, unless otherwise stated.

The suboesophageal and the terminal, or 8th, abdominal ganglia are, as already mentioned, compound ganglia. The threefold nature of the suboesophageal ganglion is evident in sagittal sections such as that represented in Plate 3, A. At first glance four segments appear to be indicated by the presence of four commissures and four corresponding groups of ganglion cells. Examination of other sections of this series, however, as well as of the sagittal sections of other larvae of the same age, and also of younger larvae, shows that the last two bundles of transverse nerve fibers, together with the last two cell groups, belong to the labial segment. This component of the suboesophageal ganglion shows from the first two well-defined transverse commissures, like those of the succeeding trunk ganglia (*36*, *fig. 45*), while the mandibular and maxillary divisions never show clearly more than one. In the terminal ganglion three double commissures are distinguishable, being those of the 8th, 9th, and 10th abdominal segments (*38*). The same condition is found in embryos of Forficula (*14*, *fig. 44*).

One detail in the cellular composition of the nervous system should be noted. In the peripheral region of the brain and ganglia of the ventral cord of mature larvae are to be seen here and there cells of large size, which in their mode of division and other characters are plainly to be identified as neuroblasts. This observation corresponds with those of Bauer (*2*) on the larvae of Vespa, Formica, and other insects. Hilton (*15*) also reports the presence of neuroblasts in the brain and ventral cord of the larva of Corydalis.

CORPORA ALLATA

The corpora or so-called "ganglia" allata have, as is now well known, no intimate connection or relation with the nervous system, but since they have also no connection with other organ systems it is convenient to follow the time-honored custom of considering them at this point. They have in the mature larva the same structures and relations as in the newly hatched larva (*36*). They are spherical bodies (Pl. 2, B, *CorAll*), about 0.85 mm. in diameter, situated one on each side of the mid-line, close behind the brain, lying on the dorsal side of the anterior arms of the tentorium, near their posterior ends, and in close contact with the lateral walls of the aorta. Each is composed of a compact mass of polyhedral cells having finely granular and deep-staining cytoplasm, and nuclei with abundant chromatin in the form of subspherical granules. Surrounding the corpora is a delicate membrane secreted by the outer layer of cells. Just cephalad of the corpora, on each side of the aorta, is a tuft of tracheoles. Two or three of these enter the corpora allata and may be seen here and there between the cells of the latter.

TRACHEAL SYSTEM

The external openings of the tracheal system, the spiracles (fig. 2, A, Pl. 1, D, *Sp*), are 20 in number, or 10 pairs, each of the 10 segments from the 2d trunk (thoracic) segment to the 10th (8th abdominal), inclusive, bearing one pair. They are arranged on each side in a row parallel with the long axis of the body, and very nearly midway between the ventral and dorsal mid-lines. The mesothoracic spiracles are placed near the anterior limits of that segment; in the older larvæ they are located so far cephalad that they have frequently the appearance of coming within the limits of the prothorax. The spiracles of the succeeding segments are also located near the anterior borders of their respective segments at the bottom of shallow depressions, which are continuous with the adjacent intersegmental constrictions. Each spiracle is a minute, round aperture situated in the middle of a small circular elevation of the surface, the stigma. The spiracles are connected by short branches, the spiracular branches (Pl. 3, D,

SpBr), to the tracheal trunk (fig. 2, A, *TraTr*) of the corresponding side. Each of these trunks traverses the body cavity, about midway between the hypodermis and mid-intestine, slightly ventrad to the line formed by the spiracles of that side. The tracheal trunk of a mature larva has an inside diameter of about 0.1 mm. in its posterior and larger half; in the three anterior segments its diameter is reduced to about one-half of this caliber. The anterior ends of the tracheal trunks of opposite sides meet to form a loop, the anterior transverse commissure (fig. 2, A and B, *ATral*), in the region of the neck and above the oesophagus; a similar loop, the posterior transverse commissure (fig. 2, A, *PTraL*), is formed by the posterior ends of the tracheal trunks. This latter, however, is situated ventrad of the posterior end of the mid-intestine, near its junction with the hind intestine. The two tracheal trunks are also united by a segmentally arranged series of transverse commissures, which lie in the ventral half of the body cavity, close to the body wall, passing below the ventral nerve cord. In a larva three days old or more the prothorax is seen (fig. 2, A) to possess one commissure, while the mesothoracic, metathoracic, and first abdominal (propodeal) segments each possess two commissures. These, however, become confluent just before their junction with the tracheal trunks. It should be noted that the commissures in the thoracic segments are quite slender, while those in the 1st abdominal segment approximate the diameter of the tracheal trunks at this point. In the 2d to the 8th abdominal segments the transverse commissures are single and of large diameter, the most anterior being largest, while the transverse commissure of the 9th abdominal segment is relatively slender and its course somewhat oblique. The prothoracic commissure joins the tracheal trunks just in front of the branches from the mesothoracic spiracles, those of the mesothorax just behind these branches. The commissures of the other segments, except that of the 9th segment, join the tracheal trunks either close to or slightly caudad to the corresponding spiracular branches.

Throughout their length the tracheal trunks give off numerous branches which supply the various regions of the body. Three branches on each side supply the head. The more anterior of these (fig. 2, B, *Bra1*) arises from the anterior transverse commissure close to the mid-line and runs cephalad to the brain, passing beneath the base of the optic lobes. It then turns abruptly dorsad, and supplies the anterior face of the brain and the region immediately adjacent (*a*). In the latter part of its course it passes close to and in contact with the spine, which arises from the anterior arm of the tentorium on each side. The second branch (*Bra2*) is much larger and arises from the anterior face of the transverse commissure a short distance ectad of the branch just described. Near its base it gives off a secondary branch (*b*) which passes mesiad and cephalad above the brain between the two halves of the protocerebrum, and supplies the aorta and the brain in the region of the mushroom bodies. The main branch takes a straight course cephalad and slightly ventrad, below the optic lobe, to the anterior region of the head, where it divides into three secondary branches. One of these (*c*) curves abruptly dorsad and breaks up into a large number of tracheoles at the base of the antennal rudiment. Before terminating its course, however, it gives off a twig to the mandible and one to the labrum. The second secondary branch passes mesiad to the head cavity underlying the supraoesophageal ganglion. The third secondary branch (*d*) supplies the maxilla.

In the prothorax the only tracheal branch worth noting is one (fig. 2, B, *e*) which arises on each side from the single tracheal commissure of this segment near its junction with the tracheal trunk, and passes mesiad and cephalad to supply the walls of the salivary glands in the region of the neck. In the remaining trunk segments, exclusive of the 9th and 10th abdominal, the number and arrangement of the tracheal branches is virtually identical. Springing from the

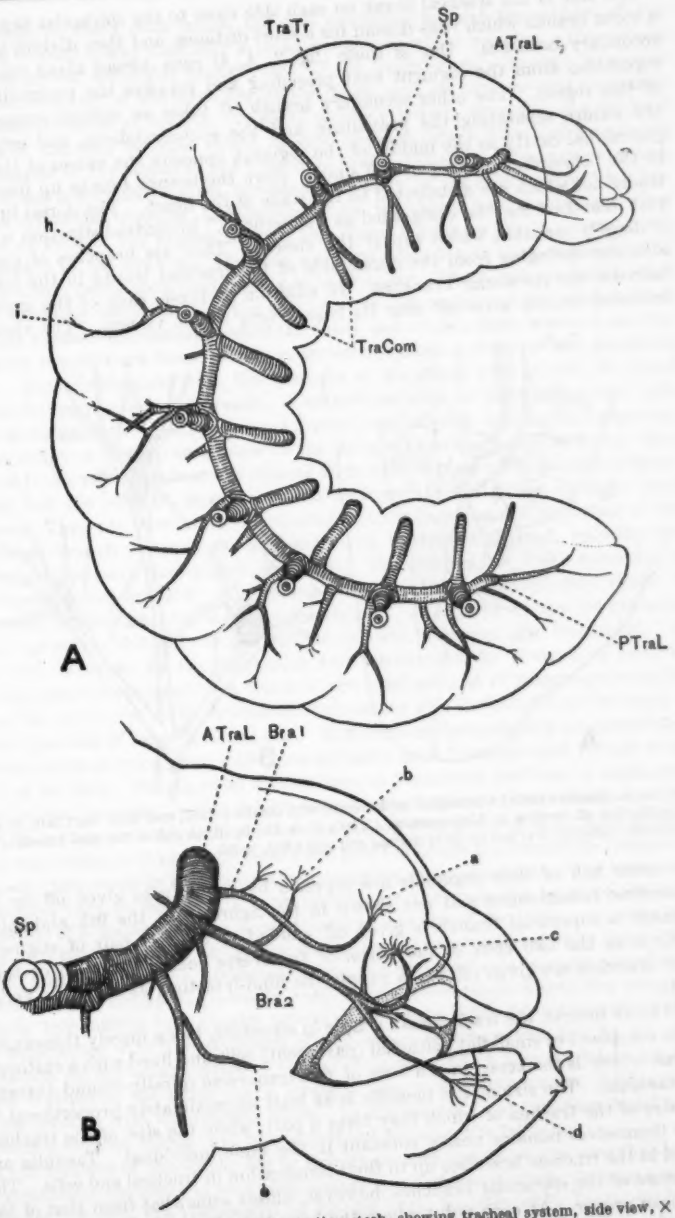

FIG. 2.—A, honeybee larva treated with caustic potash, showing tracheal system, side view, × 18; B, head of larva treated with caustic potash, right side, showing distribution of tracheae, × 44

dorsal side of the tracheal trunk on each side close to the spiracular branches is a stout branch which runs dorsad for a short distance, and then divides into two secondary branches. One of these (fig. 2, A, *h*) runs dorsad along the line of separation from the segment next preceding and supplies the pericardial cells of this region. The other secondary branch (*i*) takes an oblique course along the suture separating the prescutum and the scutoscutellum, and enters the pericardial cavity in the middle of the segment opposite the valves of the heart in the pericardial intersegmental sinus. Here the branch breaks up into a few tracheoles which are distributed to the walls of the heart. The dorsal branches just described may be designated as "superficial," in contradistinction to other ("deep") branches which supply the viscera. They are branches of considerable size springing from the dorsal side of the tracheal trunks in the intervals between the spiracular branches. In addition to these, each of the superficial branches usually gives off near its base a twig to the viscera. The viscera in

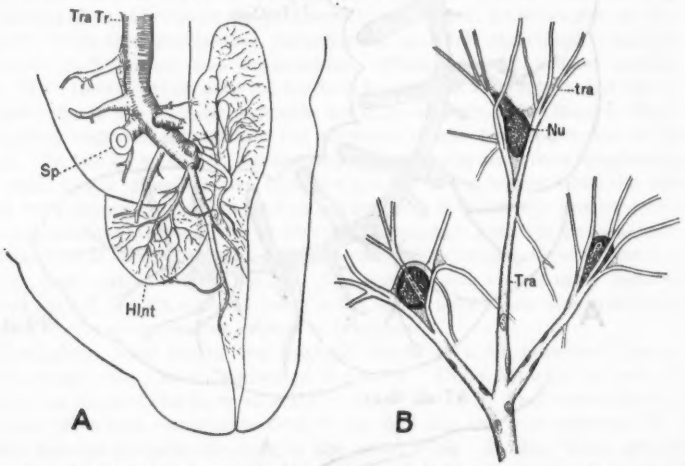

FIG. 3.—A, posterior end of a honeybee larva treated with caustic potash, seen from right side, showing distribution of tracheae to hind-intestine (*HInt*), × *ca* 33; B, distal end of tracheal branch (*Tra*) showing tracheoles (*tra*) and nuclei of tracheal end cells (*Nu*), × 195

the lower half of their segments are supplied by small twigs given off by the transverse commissures and not shown in the figures. In the 9th abdominal segment a superficial branch is given off caudad of the last pair of stigmata, while from the two ends of the posterior transverse commissure two or three deep branches are given off which supply the hind-intestine, as shown in Figure 3, A.

As in all insects, the tracheae are simple in structure, being merely thin-walled tubes composed of small flat epithelial (pavement) cells and lined with a chitinous intima which is thickened in the form of fine transverse spirally-wound threads, the taenidia. The size of the taenidia is at least approximately proportional to the size of the trachea of which they form a part, while the size of the tracheal cells themselves remains nearly constant in the same individual. Taenidia are found in the tracheal branches up to their termination in tracheal end cells. The structure of the spiracular branches, however, differs somewhat from that of the tracheae proper. At each point where the hypodermal epithelium turns inward to become the wall of a spiracular branch it forms a sharp fold, thus somewhat reducing the mouth of the aperture (Pl. 3, D). The chitinous cuticle also folds

upon itself at every such point, the fold extending toward the middle of the opening in such a way that only a small circular aperture remains. The cells of the wall of the spiracular branch next to the hypodermis, although long-prismatic in form, are of the same size as the latter, and are also covered internally by a smooth layer of cuticle. A short distance within, however, the internal surface of the wall becomes raised up into annular ridges, thus again reducing the diameter of the lumen of the branch so that a distinct antechamber is made, more or less spheroidal in form, bounded externally by the chitinous fold bordering the spiracular opening, and internally by the ridges just mentioned. The section or zone of the branch bearing the ridges comprises about a half of the total length of the branch. The cells are here much larger than elsewhere and usually much vacuolated, particularly at their bases. The ridges are here formed not so much by thickenings of the cuticle as by the contour of the inner ends of the cells themselves, except toward the inner end of this zone, where a number of coarse taenidia are found which in sections present a more or less pinnatifid form. These intergrade with the taenidia of the usual type which are found farther centrad within the branch. Centrad the zone of large cells rather suddenly gives place to the flat pavement type of cells common to tracheae in general. The description just given applies to the larva of intermediate size, about three days old. In mature larvae the zone of large cells is even more sharply differentiated, but the cells no longer combine to form annular ridges on their inner surface. They are very much vacuolated at their bases, and this portion of the spiracular branch presents the appearance of having contracted, reducing the lumen to little more than a cleft (fig. 3, B). The significance of this reduction of the lumen is not evident. The general aspect and the arborescent mode of branching of the tracheae is shown in Figure 3, A. At their tips the branches break up rather suddenly into a tuft of delicate filaments, the tracheoles. At the point of origin of the tracheoles and surrounded by them is a nucleus, of large size as compared with those of the tracheae and of somewhat irregular form (fig. 3, B, *Nu*). Its chromatin is abundant and distributed in the form of coarse granules of fairly uniform size. Surrounding the nucleus is an exceedingly delicate layer of cytoplasm, which accompanies each tracheole and in fact forms part of its wall. This is most clearly seen in transverse sections of tracheoles. The intima, however, is that which gives to the tracheoles their sharp contour, and since they are still visible in caustic potash preparations it is to be inferred that this intima is chitinous. Near their point of origin the tracheoles frequently branch; farther on in their course branching becomes infrequent. The tracheoles of course vary in length. In a preparation of the muscular layer of the mid-intestine of a mature larva a single tracheole was traced for a distance of 0.548+ mm. In the pericardial cavity the tracheoles are much shorter than this (about 0.300 mm.). After the preliminary branching a tracheole is quite uniform in diameter, and decreases gradually until the double contour is lost, the tracheole finally terminating in a slender point. The course taken by a tracheole differs in accordance with the structure of the organ or tissue supplied by it. For example, on the outer surface of the mid-intestine, which is very richly supplied with tracheoles, the latter run in straight lines or in gentle curves, the majority being parallel with the circular fibers. In the fat body, on the other hand, they pursue a sinuous course, winding in and out between the fat cells.

The relation of the tracheoles to the organs and tissues of the honeybee larva is essentially the same in every case, since nowhere has a tracheole been seen to penetrate a cell, the statements of Leydig (*32*), Kupffer (*30*), Lidth de Jeude (*33*), Gilson (*12*), and Holmgren (*16*) to the contrary notwithstanding. In the case of the alimentary canal and the heart the tracheoles simply spread out over

the external surface. On the other hand, the brain, ventral cord, and ovaries are not only penetrated by the tracheoles but not infrequently by the finer tracheal branches also, the latter terminating in end cells, which therefore lie within the tissues of the nervous system or of the ovaries, as the case may be. Anastomosis of the tracheoles to form a meshwork, as reported by Wielowieyski (*51*), Von Wistinghausen (*54*), Petersen (*41*), Williams (*53*), and others was not observed.

The tracheal system of the bee larva offers nothing of special interest in its general form and relations and conforms to the type usual in the higher insects. As compared with the imago the tracheal system is simpler and more generalized. In the abdomen of the imago, however, particularly in segments 3 to 7, the tracheal trunks and their metamerically arranged commissures and branches may easily be recognized, although now enlarged to form air sacs (*46*). The posterior commissure is wanting. In the thorax the tracheal system is more greatly modified, and the larval type correspondingly obscured.

ALIMENTARY CANAL, MALPIGHIAN TUBULES, AND SILK GLANDS

ALIMENTARY CANAL

The alimentary canal comprises a short and slender fore-intestine (Pl. 4, A, *Oe*), a voluminous mid-intestine (*MInt*) and a relatively short hind-intestine, having a sigmoid flexure (*HInt*).

The fore-intestine shows the usual differentiation into three subdivisions, mouth, pharynx, and oesophagus.

The mouth (Pl. 2, B, *Mth*) is a narrow transverse slit bounded above by the clypeus, below by the labium, and laterally by the mandibles. It opens immediately into the pharynx. This is a somewhat ill-defined region, comprising the anterior end of the fore-intestine and extending caudad to about the point where the crura cerebri cross the fore-intestine. The epithelium of the mouth and pharynx (with the exception of the roof of the latter) is precisely similar to the hypodermis of adjacent parts of the head, being composed of closely crowded prismatic cells with flat external ends (Pl. 2, B, and 4, C). On the roof of the pharynx is a conspicuous and well developed epipharynx (Pl. 3, A, and 4, C, *Ephy*), which extends from the mouth well back into the oesophagus. It is broad and flat at its anterior end (Pl. 3, A, *Ephy*), scarcely rising above the level of the adjacent epithelium of the roof of the mouth, but in the pharyngeal region it becomes a highly convex fold of the dorsal wall, projecting ventrad into the lumen of the pharynx and giving the latter a crescentic outline in transverse section (Pl. 4, C, *Ephy*). The cells constituting this fold are very different from those of the remainder of the pharyngeal wall, being of small size and elongated, pyriform or club-shaped in form, their larger ends directed toward the lumen of the oesophagus. On the dorsal surface of the pharynx the cavity of the epipharyngeal fold is crossed by a large number of muscle fibers which unite the two lateral edges of the fold. These are shown in Plate 4, C, and in section in Plate 3, A, *EphyMcl*. Beneath these are a few longitudinal muscle fibers.

On the floor of the pharynx, at its external end, is a small papillate elevation, provisionally labeled the hypopharynx (Pl. 3, A, *Hyphy*).

In addition to the muscles of the epipharynx, the pharynx is provided with other muscles, which are described in this paragraph. In the clypeus a pair of small muscles take their origin from the dorsal wall and are inserted on the epipharyngeal fold close to the median plane. Some four or five pairs of similar muscles are ranged behind one another, having their origin on the dorsal wall of the labrum. These are the levators of the epipharynx (Pl. 4, C, and 6, C, *LevEphy*). Their action is evidently directly opposed to those crossing the

epipharyngeal fold, which, by drawing together the two edges of the fold, force the epipharynx down into the lumen of the pharynx and thus occlude it, while the levators, on the other hand, virtually serve as dilators. A larger pair of muscles having their origin on the dorsal wall of the labrum are inserted on the oesophagus at the lateral margins of the epipharynx, the levators of the pharynx (Pl. 4, C, *LevPhy*). Just ectad of these are inserted still another pair of muscles which are attached to the cranial wall on each side of the base of the labrum, the superior dilators of the pharynx (Pl. 4, C, *SDilPhy*). On the ventral side of the pharynx is a group of muscles having their origin on the anterior face of the central body of the tentorium, which are inserted on the ventral wall of the pharynx. These are the inferior dilators of the pharynx (Pl. 3, A, *DilPhy*). This list comprises the total equipment of muscles possessed by the pharynx.

The pharynx passes without material change in caliber into the oesophagus. This is a cylindrical tube, its walls continuous with those of the pharynx, but formed of cells of a somewhat different character, these being much less crowded than those of the pharynx and varying in form from cuboid to long columnar. Their central ends are rounded instead of flat. This epithelial layer, however, does not always form a true hollow cylinder, being generally more or less infolded at the sides, top and bottom, and the cells being higher at these points, so that the lumen of the oesophagus is frequently quadrangular in section (Pl. 2 A, *Oe*), or even in some cases rosette-shaped. A chitinous cuticle, continuous with that covering the external surface, lines the oesophagus as well as the mouth and pharynx. In the anterior part of the fore-intestine this corresponds in thickness with the external cuticle, but toward the posterior end of the fore-intestine it becomes thinner, and in sections has a much wrinkled and torn appearance. It usually extends a short distance into the lumen of the mid-intestine, forming the "funnel" (Trichter) of Schneider (*45*). On its external surface the oesophagus is clothed with a single layer of circular (transverse) muscle fibers. Longitudinal muscle fibers appear to be virtually absent. The caudal end of the oesophagus, where it joins the anterior end of the mid-intestine, is reflected back on itself to form an oesophageal valve (Pl. 3, A and 5, C, *OeVlv*) similar to that found in many other insects. The cells of that part of the valve which is reflected back are notable for their attenuated, almost linear form. Muscle cells are lacking between the two folds of the valve.

The mid-intestine (Pl. 4, A, *MInt*) has the form of a long hollow cylinder with rounded ends, and in mature larvae has a diameter about one-third of that of the body. It extends from the prothorax to the ninth abdominal segment. It is hardly necessary to state that structurally the mid-intestine is a blind sac, the posterior end being completely closed. It is anchored in place by numerous tracheae which extend mesiad from the longitudinal trunks. The finer branches of these tracheae terminate in tracheal end cells upon reaching the surface of the mid-intestine. From these end cells numerous tracheoles are sent out enveloping the external surface of the mid-intestine. If the muscular coat of the intestine be stripped off, as can be done in favorable cases, its surface is seen to be closely and uniformly dotted with tracheal end cells, one of which is represented in Plate 5, D, *TraECl*.

The walls of the mid-intestine are composed of a thick single-layered epithelium covered externally by a delicate meshwork of muscle fibers. The cells composing the epithelium (with the exception of a few cells around the anterior end, next to the oesophageal valve) are all alike, being relatively large and having in general a short and rather cubical form, their mesial margins, however, being slightly convex (Pl. 5, B). Here and there are to be seen cells which are pyriform, with their larger ends directed centrad and projecting into the lumen.

There is, however, no evidence that cells or parts of cells of the epithelium are set free in the lumen, as described by Snodgrass (*46*) for the imago. The cytoplasm of the cells of the mid-intestine is always deeply stained in sections (Pl. 5, A, *MInt*) and has the appearance of being traversed by numerous parallel fibrillae which run at right angles to the surface of the epithelium. A similar appearance is found in the secreting cells of the silk gland in certain Lepidoptera (*12*) and in the epithelial cells of the mid-intestine of Ptychoptera (*11*). The nuclei are spherical, as a rule, and contain a large number of chromatin granules. In fixed material, at least, these granules, along with the achromatic material, are agglomerated into a dense spherical mass within the nuclear membrane, leaving a peripheral space vacant. This condition may, however, be an artifact. On their mesial surfaces the cells of the mid-intestinal epithelium show a well-developed striated border (Pl. 5, B, *StrBor*) similar to that observed in Ptychoptera (*11*) and other insects. Wedged in between the bases of the cells, next to the basal membrane (intima) triangular groups of minute cells are seen here and there. These are the imaginal cells of the mid-intestine (Pl. 5, B, and C, *ImCls*).

The mid-intestine is lined throughout by a homogeneous layer of unknown chemical nature, apparently of gelatinous consistency, and having a thickness two or three times that of the epithelium, the so-called "peritrophic membrane" (Pl. 5, C, *Pmb*). In sections it is more or less finely granular in structure. Peripherally it is in intimate contact with the epithelium of the intestine; centrally it is sharply demarcated from the enclosed food mass. Not a little has been written concerning this somewhat problematical structure in various insects, but a full review of the literature will not be attempted here. Rengel (*44*) has described it in the larvae of the wasp (Vespa) and honeybee, Strindberg (*47*) in the ant embryo, and Snodgrass (*46*) and Petersen (*41*) in the adult honeybee. Rengel states that in larvae the peritrophic membrane has a laminated structure consisting of several concentrically arranged membranes, as is plainly the case in the adult, but in all of the writer's preparations of this membrane he has never observed this structure except at the anterior end of the mid-intestine. Elsewhere the membrane is thick and homogeneous, but here the epithelial cells grow rapidly and progressively smaller, forming a ring around the oesophageal valve (Pl. 5, C, *x*) and are separated from the latter by a narrow space. These cells also differ from those of the remainder of the mid-intestine not only in being of smaller size but also in lacking, at least to a large extent, the striated appearance of the cytoplasm. From the surface of these cells thin streams of secretion can plainly be seen running caudad and joining with the principal mass of the peritrophic membrane within the mid-intestine. Streams of this material also appear leading inward from the three rows of epithelial cells next to the ring of smaller cells, as shown in Plate 5, C, and this appearance is characteristic of all of the sagittal sections examined, including preparations of both young and old larvae. It suggests that the cells of the anterior rim and those of the two or three adjacent rows are responsible for the secretion of the peritrophic membrane; an interpretation precisely in line with the view advanced by Van Gehuchten (*11*) in the case of the dipterous larva Ptychoptera and Cuénot (*8*) in Orthoptera. Strindberg, however, has advanced against this view the fact that in the ant larva peritrophic membrane is continuous over the closed posterior end of the mid-intestine, which, he states, could not be the case if the membrane were secreted by an anterior rim of cells. This objection, however, would have less weight if, as seems probable, the peritrophic membrane is fluid or semi-fluid, since from its nature it would tend to form a uniform layer over the area of contact and therefore would flow together over the posterior end. It should be noted that the peritrophic membrane described above has nothing whatever to do with the cuticle secreted by the oesophagus, the free

posterior ends of which frequently project far into the anterior end of the mid-intestine (Pl. 5, C, *Ctl*).

The external surface of the mid-intestine, as already stated, is covered by a delicate network of muscle fibers. A small portion of this sheet, stripped off from the mid-intestine, is shown in Plate 5, D. The central or inner surface is uppermost. The inner layer (*LMcl*) is composed of branched muscle cells whose delicate processes, connecting adjacent cells and thus forming an anastomising plexus, tend to run in a longitudinal direction. Below these, and morphologically outside of them, is a layer of transverse muscle fibers (*TMcl*). These are closely and uniformly spaced, and are also quite uniform in caliber. The nuclei of the cells composing this layer are much smaller than those of the inner layer. The muscle cells of the transverse layer are also interconnected by extremely delicate protoplasmic processes, some of which are indicated in the figure.

The hind-intestine (Pl. 4, A, *HInt*) is a cylindrical tube of fairly uniform diameter except at its anterior end, where it shows a funnel-like or bell-shaped expansion, the larger end of which is applied to the posterior end of the mid-intestine. From this point it bends ventrad, taking a cephalad course to the sixth abdominal segment, where it bends sharply upon itself and takes a direct course caudad to its termination on the tenth abdominal segment. The hind-intestine of the honeybee larva exhibits a simpler structure than that of the ant larva, in which the posterior portion of the hind-intestine is enlarged, narrowing again near the anus, three divisions being thus formed, small intestine, large intestine and rectum (*35*). This condition also exists in the larva of the beetle Anobium (*23*).

As already stated, the anterior end of the hind-intestine exhibits a funnel-like or bell-like enlargement (Pl. 4, A). The end of the funnel is, however, not open, but is closed by an extremely thin layer of minute cells (Pl. 6, A, *dph*), which is continuous around the margin of the funnel with the epithelial wall of the mid-intestine. This epithelium, on the sides of the funnel-like enlarged portion, is thick and composed of a large number of slender club-shaped cells (Pl. 6, A, *HInt*). These give place, at the neck of the funnel, to larger prismatic or columnar cells. The remainder of the epithelium of the hind-intestine is formed of cells of this type. This is thrown into deep folds, as shown in Plate 5, E, projecting almost to the center of the lumen and giving the latter a stellate aspect in section. Relatively stout muscle fibers (*TMcl*) encircle the hind-intestine, being found from the margin of the funnel-like expansion to the anus. These are for the most part arranged in a single layer, but toward the posterior end they become more numerous and are arranged in two or even three layers. Outside of the transverse muscles are a few irregularly arranged longitudinal fibers (Pl. 5, E, *LMcl*). In the 10th segment numerous slender muscle fibers run between the lateral hypodermis and the lateral walls of the hind-intestine.

The posterior termination of the hind-intestine, the anus, is a simple transverse slit situated on a slight elevation in the center of the 10th abdominal segment.

The mode of attachment of the mid- and hind-intestines in the larvae of the aculeate Hymenoptera is of special interest and has been studied and described in detail by Rengel (*44*) in the wasp (Vespa), in the ant (Lasius) and in the honeybee. With the exception of minor details, it is the same in the three groups. As shown in Plate 6, A, at the extreme posterior end or fundus of the mid-intestine there is an outpushing (*st*) of the epithelium, thus forming a rounded projection on the external surface of the fundus. In Vespa this projection is quite prominent, forming the "stalk" (Stiel) of Rengel. In the honeybee larva it is externally merely a low rounded eminence; internally it is represented by a depression of the epithelium, the bottom of which is formed by a heap of irregular transparent cells,

smaller than those of the adjacent epithelium. The muscular investment of the mid-intestine (*MclEnt*) ceases abruptly at the margin of the "stalk." As already stated, the enlarged anterior end of the hind-intestine is closed by a thin layer of minute cells, forming a circular structure (*dph*) which may conveniently be termed "the diaphragm." The central part of the diaphragm is closely adherent to the stalk, as described by Rengel. In larvae of Vespa and of ants the diaphragm is relatively much thicker than in those of the honeybee, judging from the figures given by Rengel (*44*), Karavaev (*22*) and Pérez (*40*), but otherwise the relations are essentially similar.

MALPIGHIAN TUBULES

The Malpighian tubules are four in number and lie, two on each side, between the lateral faces of the mid-intestine and the body wall (Pl. 4, A and 5, A, *Mal*). They pursue a winding course, being thrown into numerous loops and folds, and extend from about the last thoracic to the 9th abdominal segment. In the newly hatched larva the tubules are slender and of nearly uniform diameter throughout; in the mature larva their anterior ends only are slender, the tubules widening gradually caudad, reaching their maximum diameter, which is about one-half that of the mid-intestine, in the region of the 7th abdominal segment (Pl. 4, A, *Mal*). From this point they taper rapidly to their caudal (or central) ends, which are inserted, two on each side, between the mid-intestine and hind-intestine where the two latter have their junction. These central ends are exceedingly slender and pointed, composed of relatively small cells, and become closely attached to the thin epithelium closing the anterior end of the hind-intestine, with their tips abutting on the stalk of the hind-intestine (Pl. 6, A, *Mal*). The lumen of the Malpighian tubules becomes greatly reduced here and finally ceases, the central ends of the tubules therefore ending blindly, contrary to the statements commonly found in the literature on this subject (*44*). The writer (*36*) stated that in the newly hatched larva the Malpighian tubules open into the mid-intestine, but renewed investigation shows that there is no basis for the statement, since in all the sections examined, both cross and sagittal, the central ends of the tubules disappear in the relatively thick layer of cells closing the anterior end of the hind-intestine. Sections of a larva two days old also fail to disclose any connection between the lumen of the Malpighian tubules and that of the hind-intestine.

The walls of the Malpighian tubules consist of a single layer of epithelial cells. In very young larvae the wall of the tubules is relatively thick and the centrally placed lumen correspondingly small. In mature larvae the cells composing the walls are flat, thin, and pavement-like in character (Pl. 5, A, *Mal*, and Pl. 4, B and D). This condition exists even in the slender anterior ends, clearly indicating that the tubules are distended by internal pressure. The nuclei are discoid (Pl. 4, D, *Nu*), being flattened in a plane normal to the surfaces of the tubules, and contain abundant chromatin in the form of subequal spherules. The cytoplasm of the cells displays no fibrillae, as in the case of the cells of the mid-intestine and silk glands, and appears to be finely granular. The margins of the cells at the point of junction with one another are uniformly vacuolated, as shown in Plate 4, D, thus giving the tubules, stained or unstained, a characteristic mottled appearance in surface view (Pl. 4, B). The tubules are lined within by a cuticular intima, possibly chitinous, which stains much less densely than the cytoplasm (Pl. 4, D, *Int*).

The condition just described is characteristic of larvae shortly before the capping of the wax cell. Younger larvae show intermediate conditions, that is, the diameter of the tubules is relatively smaller and the walls thicker. The

next phase in their development takes place subsequent to capping and is directly correlated with the establishment of communication between the lumina of the mid- and hind-intestines, and the consequent evacuation of the feces. This takes place some time during the twenty-four hours subsequent to capping, and has been treated at length by Rengel (*44*). In brief it consists, as shown in Plate 6, A and B, in an outpushing (caudad) of the fundus of the mid-intestine, that is, of the stalk, into the lumen of the anterior enlarged end of the hind-intestine and the subsequent perforation of the stalk and also of the diaphragm to form a tubular opening through which the fecal accumulations of the mid-intestine are forced by contractions of the latter. This mass of feces is omitted in Plate 6, B. In larvae of this stage the central ends of the Malpighian tubules no longer end blindly, but each now opens into the hind-intestine by a minute pore-like aperture. These openings are close to the junction of the mid- and hind-intestines, as shown on the left side in Plate 6, B, *Mal.* The appearance of this and other preparations suggests that the central ends of the tubules have perforated the diaphragm while at the same time their lumina became extended to communicate with that of the hind-intestine. A curious feature of the efferent ducts of the Malpighian tubules of this stage is the appearance of structures which in fixed preparations resemble motile cilia. That the Malpighian tubules are now emptying themselves of their contents is strikingly shown by sections of the tubules at points more or less remote from the place of attachment. Whereas in sections of mature larvae prior to the establishment of communication between the mid- and hind-intestines the Malpighian tubules have in general the appearance of thin-walled tubular sacs, they now show a much diminished caliber and the cells forming the walls are no longer flat, but are cubical in form.

The accumulation of solid excreta in the blind mid-intestine of the bee larva is therefore paralleled by the accumulation of fluid excreta (urates?) in the blind Malpighian tubules. Both discharge their accumulations at the same time. The advantage of this in the life history of the larvae is obvious.

The imaginal Malpighian tubules appear just previous to capping (Pl. 6, A and B, *mal*), as outgrowths of the anterior enlarged section of the hind-intestine (*1*).

SILK GLANDS

The silk glands comprise a pair of slender cylindrical tubules, thrown into numerous short convolutions, and extending from the posterior border of the mesothoracic segment to the neighborhood of the sixth abdominal segment (Pl. 4, A, *SlkGl*). Their location, relative to the other organs, is shown by Plate 5, A, *SlkGl*. They lie, one on each side of the mid-line, closely surrounded by fat cells, about halfway between the mid-intestine and the ventral body wall. At about the posterior margin of the mesothoracic segment the glands, strictly speaking, terminate, and each gland here opens cephalad into a thin-walled duct which pursues a straight course into the head, passing close to the ventral wall and beneath the suboesophageal ganglion, where it meets its mate from the opposite side. The two ducts unite to form a common duct (Pl. 2, A, *SlkD*) which terminates on the tip of the labrum. The common duct is cylindrical with the exception of its anterior end, where it rather suddenly widens out laterally and opens by a narrow transverse slit on an elevation, also transversely elongated, situated on the tip of the labrum (Pl. 1, F, and 3, A, *SlkDO*).

The finer structure of the silk glands is illustrated by Plate 5, F and G. Plate 5, F, represents an oblique transverse section through one of the silk glands near its posterior end. The cells forming the wall of the tube are in many respects similar to those forming the mid-intestinal epithelium, although much smaller, the nuclei of the walls of the silk gland having a diameter scarcely more than a

third of that of the nuclei of the mid-intestinal epithelium. The cells forming the walls of the silk gland are like those of the mid-intestine in the deeply-staining character of their cytoplasm, which usually stains so densely in comparison with the other tissues as to be almost totally opaque, as shown in Plate 5, A, *SlkGl*. Other points of similarity are the form of the cells, whose breadth and height are approximately equal, the striated or fibrillated aspect of the cytoplasm, noted also in the cells of the silk gland of Lepidoptera and Trichoptera (*12*), and the spherical nuclei, each containing a compact mass of chromatin granules. Near their anterior ends the character of the cells forming the wall changes somewhat. Here the walls are thicker, the cells composing them being smaller and long-columnar in form. The cytoplasm stains less deeply and no longer shows well-marked fibrillae. The lumen of this portion of the gland shows within it coagulated secretion, although the larva in question was scarcely mature.

The ducts of the silk glands are thin-walled and otherwise histologically precisely similar to the tracheae, this similarity extending to the possession of a chitinous intima, thickened spirally to form taenidia.

MUSCULAR SYSTEM

MUSCLES OF THE HEAD

The muscles of the bee larva may be divided for descriptive purposes into muscles of the head and muscles of the trunk, since these two sets are totally different. The principal muscles of the head are as follows:

MANDIBLES

Each of these is provided with an extensor and a flexor muscle. The extensor (Pl. 6, C and D, *EMd*) is inserted on the inner surface of a papillate elevation of the hypodermis located on the ectal side of the base of the mandible. From this point it passes directly caudad to its origin on the fold of hypodermis separating the head and trunk (neck fold) close to the outer end of the transverse arm of the tentorium. The flexor muscle (Pl. 6, C and D, *RMd*), which is the largest in the head, is inserted on a long and pointed hollow spine, the mandibular apodeme (Pl. 1, A, and 6, D, *RAp*), which arises from the mesial side of the base of the mandible (*Md*). From this a stout bundle of muscle fibers passes caudad parallel to the fibers of the extensor muscle to an origin just dorsad of them. Another and larger group of fibers breaks up into small subequal bundles, passing behind the brain. These are attached at regular intervals along the neck fold between the point of origin of the extensor muscle and the mid-dorsal line of the head (Pl. 6, C, *RMd*).

MAXILLAE

Mesiad and dorsad of the base of each maxilla, below the apodeme for the extensor of the mandible, there is a papillate elevation of the hypodermis, on the inner surface of which is inserted the flexor muscle of the maxilla. This is of small size (Pl. 6, C, *RMx*), and originates on the neck fold, just ventrad of the origin of the extensor muscle of the mandible. The maxillae have no extensor muscles corresponding morphologically to those of the mandibles. They are, however, provided with a pair of strong muscles which appear to be functionally extensor muscles. Each of these takes its origin as a broad band from the ventral surface of the anterior arm of the tentorium of the corresponding side, close to the posterior end of the arm, and from here passes ectad and ventrad

to an insertion on the ventro-lateral surface of the head, just caudad of the base of the maxilla (Pl. 6, C, *EMx*). It apparently serves to rotate the maxilla outward.

LABIUM

The labium is provided with two pairs of retractors. The larger or major retractors (Pl. 6, C, *lRLb*) take their origin from the neck fold just ventrad of the external ends of the transverse arms of the tentorium. From there they run cephalad, converging meanwhile, and are inserted, a short distance apart on either side of the ventral mid-line, on the posterior margin of the labium. These muscles by their contraction withdraw the labium into the ventral part of the head. The minor retractors (Pl. 6, C, *2RLb*) are slender muscles which have their origin directly cephalad of the insertions of the major retractors. From here they run cephalad, converging at the same angle as the major retractors, to the tip of the labium where they are inserted on the wall of the common duct of the silk gland. These muscles serve to retract the tip of the labium. The two sets of retractors, when seen from the ventral surface, form a figure resembling the letter V, inverted.

LABRUM

At the base of the clypeus is a pair of well defined muscles (Pl. 2, B, and 6, C, *ClpMcl*), each of which takes its origin from the head capsule at the dorsal margin of the line of junction with the anterior arms of the tentorium. From these points the two muscles pass dorsad and slightly mesiad to insertions on minute apodemes on the dorsal wall of the head capsule, near the mid-line, at the base of the clypeus. These insertions are marked on the exterior by shallow depressions of the surface (see Pl. 1, F). Immediately cephalad of the insertions of these muscles, a second pair of muscles, the retractors of the labrum (Pl. 3, A, and 6, C, *RLm*), have their origin. These are inserted on the posterior edge of the clypeus in the dorsal mid-line.

Certain other muscles located in the labrum and clypeus and associated with the pharynx are described in the section on the alimentary canal (see p. 1184).

CRANIAL MUSCLES

Two other pairs of muscles are found in the head which pass from the tentorium to the cranial wall. The muscles of the first pair are slender, and originate on the dorsal surface of the anterior arms of the tentorium, near the junction of the latter with the transverse bar. These two muscles then pass dorsad on either side of the œsophagus, between the two halves of the brain, and are inserted on the median fold of the dorsal cranial wall. It is worthy of note that in preparations of larvae which have completed their growth these muscles appear to have lost their attachment to the dorsal cranial wall. This change is presumably related in some way to the approaching metamorphosis. The muscles of the second pair are also well developed in young larvae, but insignificant in older ones. Each of these muscles takes its origin from a long spur on the dorsolateral face of each of the anterior arms of the tentorium (Pl. 1, A, *ApTen*). These spurs are directed dorsad and laterad. In the young larvae the muscle fibers are directed dorsad and laterad, diverging meanwhile, and have broad insertions on the lateral walls of the head capsule, laterad of the cerebral lobes (*36*). In old larvae the spurs are long and directed cephalad and dorsad, extending nearly to the anterior cranial wall (Pl. 6, D), the short gap being bridged by a few muscle fibers inserted on the anterior wall of the cranium just dorsad of the antennal rudiments. The points of insertion are marked externally by well-defined circular depressions (see Pl. 1, F). Kirmayer (*26*) finds similar spurs on the tentorium and corresponding muscles in the head of the Vespa larva.

MUSCLES OF THE TRUNK

The muscles of the trunk have a strictly metameric arrangement and conform more or less closely to a definite and typical arrangement in all segments. The arrangement of the muscles in the thorax differs slightly from that of the abdominal muscles. In the abdomen the same arrangement of muscles prevails in all the segments with the exception of the 10th. In the 10th segment the muscles characteristic of the other segments are almost entirely wanting, the only

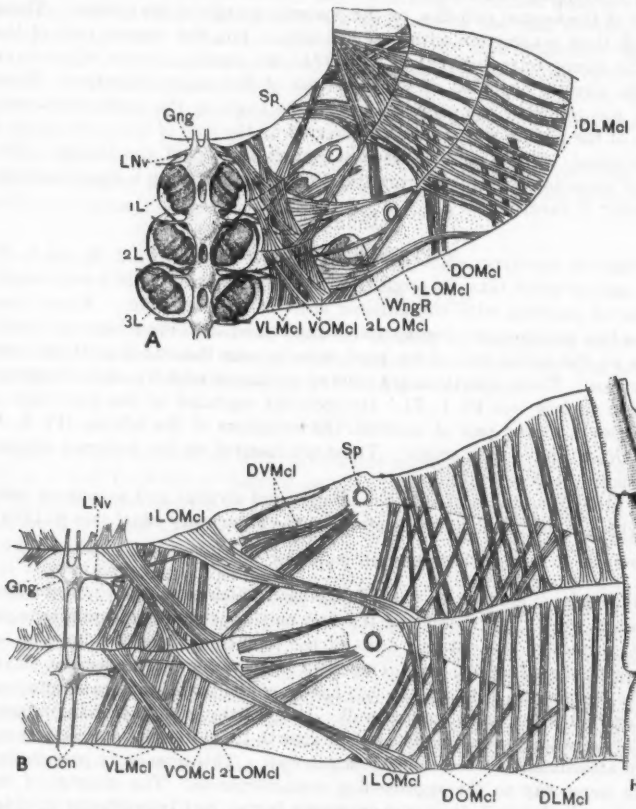

FIG. 4.—A, inner surface of right half of body wall of thoracic segments, showing musculature, × 10; B, inner surface of right half of body wall of fourth and fifth abdominal segments, showing musculature, × 10

trunk muscles present being a few fibers running from the lateral border of the anus to the anterior (lateral) borders of the segment.

The trunk muscles, taking the 4th and 5th abdominal segments (fig. 4, *B*) as typical, are the ventral longitudinal, ventral oblique, lateral oblique, dorsoventral, dorsal longitudinal, and dorsal oblique.

VENTRAL LONGITUDINAL MUSCLES

These muscles (fig. 4, B, *VLMcl*) are not, strictly speaking, longitudinal, since they diverge slightly from the long axis of the larva in a cephalo-laterad direction.

The total effect of their action is, however, to contract the ventral surface in a longitudinal direction. They are flat bands, 10 or 12 in number, disposed on either side of the ventral mid-line, close to the hypodermis, and extend between the anterior and posterior margins of each segment.

VENTRAL OBLIQUE MUSCLES

These (*VOMcl*) overlie the ventral longitudinal muscles, crossing them at an angle of about 45 degrees and running in a cephalo-mesiad direction, also connecting the anterior and posterior borders of the segment. Each consists at its anterior end of a broad band of fibers which splits into two subequal bands at its posterior end.

LATERAL OBLIQUE MUSCLES

These include two sets of muscles, which may be designated as major oblique (*1LOMcl*) and minor oblique (*2LOMcl*). The major oblique muscles are of large size and connect the anterior and posterior borders of their respective segments. Their anterior ends are attached to the body wall directly adjacent to the line of attachment of the posterior ends of the ventral oblique muscles of the segment preceding. From this point each of these muscles runs laterad and caudad, spanning the lateral fold of that side, to an attachment on the posterior border of the segment approximately on a line with the spiracles. The minor lateral oblique muscles (*2LOMcl*) comprise two small bands lying close to the body wall under the major oblique muscles. One of these small bands is attached to the posterior margin of the segment just dorsad (ectad) of the posterior attachment of the ventral oblique muscle; the other band is attached to the body wall close in front of this point. These two bands take a dorsad and cephalad course, meanwhile diminishing in breadth to a point on the body wall just ventrad of the spiracle (*Sp*).

DORSO-VENTRAL MUSCLES

Two pairs of dorso-ventral muscles (*DVMcl*) are present in each segment. The muscles of the smaller pair run close to the anterior margin of the segment from a point just dorsad (ectad) of the anterior attachment of the major oblique muscle to an attachment on the intersegmental body wall about on a line with the spiracles. The second set of dorso-ventral muscles comprises three small muscle bands on each side of the segment, having their ventral attachment to the body wall just caudad of that of the smaller muscles just described, about one-fourth of the width of the segment from its anterior margin. Their dorsal attachment is close beside that of the minor lateral oblique muscles, below the spiracles.

DORSAL LONGITUDINAL MUSCLES

These (*DLMcl*) comprise a set of narrow bands, from 10 to 12 on each side, underlying the dorsal body wall and divided by the heart into two bilateral groups. Their arrangement is truly longitudinal and the area occupied by them extends ventrad on each side almost as far as the spiracles. These muscles connect the anterior and posterior margins of the segments.

DORSAL OBLIQUE MUSCLES

The dorsal oblique muscles (*DOMcl*) include a row of from 10 to 12 slender bands on each side. Their posterior ends are attached to the posterior margin of the segment, the line of attachment extending dorsad from a point about midway between the dorsal and ventral mid-lines halfway to the dorsal mid-line. From here these muscles run cephalad and dorsad, diverging slightly, and are attached

to the dorsal body wall of each side along the suture separating the prescutum from the scuto-scutellum and in fact determining this sutural line.

In the thoracic region (fig. 4, A) the musculature is slightly different from that of the abdomen. The ventral longitudinal and oblique muscles (*VLMcl*, *VOMcl*) are readily recognized, although here their lateral extent is reduced, especially in the prothorax. The dorsal longitudinal muscles (*DLMcl*) are present in all three thoracic segments. In the prothorax there are present two groups of dorsal oblique muscles whose arrangement may be gathered from the figure. In the mesothorax and metathorax the dorsal oblique muscles are divided into two parallel groups. A strong muscle (*2LOMcl*) crosses the lateral face of each of the three segments, running from its posterior border cephalad and dorsad to its anterior border. This muscle is absent in the abdominal region. In the meso- and metathorax a very large muscle (*1LOMcl*) is attached by a broad line of attachment to the ventral side of the segment, mesiad of the leg rudiments (*1L–3L*), and runs laterad and caudad to the posterior margin of the segment near the lateral margin of the area occupied by the dorsal longitudinal muscles. This muscle evidently corresponds to the major oblique muscles of the abdomen. In all three thoracic segments the minor lateral oblique muscles (*2LOMcl*) connect the anterior and posterior margins of their respective segments, crossing the lateral body wall in an oblique direction. It seems doubtful whether these muscles are truly homologous with the minor lateral oblique muscles of the abdominal segments. In the mesothorax and metathorax a dorso-ventral muscle spans the imaginal wing disks. This muscle is much larger in the prothorax than in the metathorax.

The effects of the contraction of the various trunk muscles may be inferred from their size, direction, and attachments. These effects may readily be seen, however, on the external surface of the larva. If the figure showing the external features of the larva (Pl. 1, D) be compared with figure 4, B, it will readily become evident that the superficial contour of the larva is determined principally, if not exclusively, by the trunk muscles. The evident division of the trunk into segments is not, as in the imago, due to the formation of sclerites, but is produced principally by the longitudinal trunk muscles, aided, of course, by the ventral oblique, the major lateral oblique, and the smaller dorso-ventral muscles. The epipleural lobes are referable to the action of the major oblique muscles, the sharp demarcation of these lobes from the sternal area being apparently due to a certain amount of rigidity imparted to the body wall in this region by the ventral longitudinal and oblique muscles, since the area occupied by these coincides with this area. The depressions in which the spiracles are located are produced by the action of the minor lateral oblique muscles, aided, of course, by the posterior set of dorso-ventral muscles. The sutural lines obliquely traversing the dorso-lateral surface of the segments are plainly to be identified with the anterior insertions of the dorsal oblique muscles.

Detailed accounts of the muscular systems of hymenopterous larvae are lacking. The account by Carrière and Bürger (*7*) of the muscular system of the mason bee and that by Anglas (*1*) of the muscular systems of Vespa and the honeybee are extremely brief. Both merely recognize dorsal and ventral longitudinal muscles, and a set of obliquely arranged dorso-ventral muscles. An examination of the accounts of the muscular systems of the larvae of other orders, such as that recently given by Forbes (*10*) for lepidopterous larvae, discloses no basis for comparison with the bee larva. The muscles of the latter are, in comparison, few and simple, as might be inferred from its mode of life.

Anglas (*1*) states that some of the larval muscles, more particularly those of the abdomen, persist with slight modification through nymphosis into the imago. A study of the muscles of the abdomen of the imago shows them to be so different

in number and arrangement from the trunk muscles of the larva that identification of any given muscle or set of muscles of the imago with those of the larva proves to be impossible without a knowledge of the intervening stages.

The general features of the histology of the larval muscles has already been given (*36*). This description applies to the newly hatched larva, but no essential changes take place during larval growth. In this account it is stated that the muscles of the young larva are not striped. However this may be, in the old larvae cross-striped muscles are the rule. Mention should be made of the constant occurrence of very distinct fibrillae, "tomomitosomes," Maziarski (*34*), "filaments de resistance," Janet (*20, p. 54*), in the hypodermal cells at the points of attachment of muscles. These fibrillae frequently assume a brush-like form, as shown in Plate 6, D, at both of the ends of the dilator of the pharynx and at the posterior ends of the mandibular muscles. The filaments bind muscle, hypodermis, and cuticle firmly together, as shown in fixed material by the clinging of the cuticle, elsewhere loosened, to the hypodermis at the points where muscles are inserted.

HEART AND BLOOD CELLS

HEART

The heart of the larva is in most respects like the less differentiated portion of the imaginal heart which is situated in the abdomen. The heart consists essentially of a slender thin-walled tube situated in the mid-line close beneath the dorsal hypodermis. It is widest (about 0.25 mm.) at its posterior end and gradually diminishes in caliber up to the anterior border of the 2d trunk (the mesothoracic) segment. Here the heart leaves the dorsal body wall and bends downward, passing beneath the anterior tracheal loop (Pl. 3, A, *Ao*), at the same time diminishing rapidly in diameter, and is continued cephalad as the aorta. The aorta is not strictly tubular but is open on the ventral side, having in transverse section the form of an inverted letter U, the free edges hanging down on each side of the oesophagus and becoming clothed on the exterior with a layer of tracheoles. At the posterior side of the brain the aorta becomes reduced in its dorso-ventral diameter to enter the narrow cleft between the oesophagus and the upper ends of the crura cerebri and finally terminates at the anterior face of the brain. The posterior end of the heart terminates blindly in the 9th abdominal segment. In life the heart is transparent, and since it is bounded on either side by the relatively opaque white fat cells, it produces externally the appearance of a dark band along the dorsal mid-line of the larva.

At the middle of trunk segments 2 to 11, inclusive, the heart is sharply constricted and is thus divided into 11 chambers. These constrictions, however, do not affect the dorsal and ventral walls of the heart, but only the lateral walls, which are in fact indented by a series of pairs of opposite V-shaped indentations the open ends of which are directed slightly caudad. At the bottom of each indentation is a linear slit; these slits constitute the ostia (fig. 5, B, *Ost*). The ostia are not, however, precisely normal to the long axis of the heart, but are slightly oblique, their dorsal ends being slightly caudad of their ventral ends.

The action of the heart is simple and similar to the heart action of many other insects. The heart walls bordering on the ostia form valvelike flaps projecting inward which allow a free inrush of blood during diastole, but which automatically close the ostia during systole. The posterior pair of flaps project inward far enough also to close the posterior ends of the heart chambers during systole, preventing a backward flow of blood. Moreover, the thickened margins of the ostia share in the contractility of the heart wall, so that probably these also possess the ability to contract the ostia and the posterior ends of the heart chambers as well, thus acting as sphincter muscles.

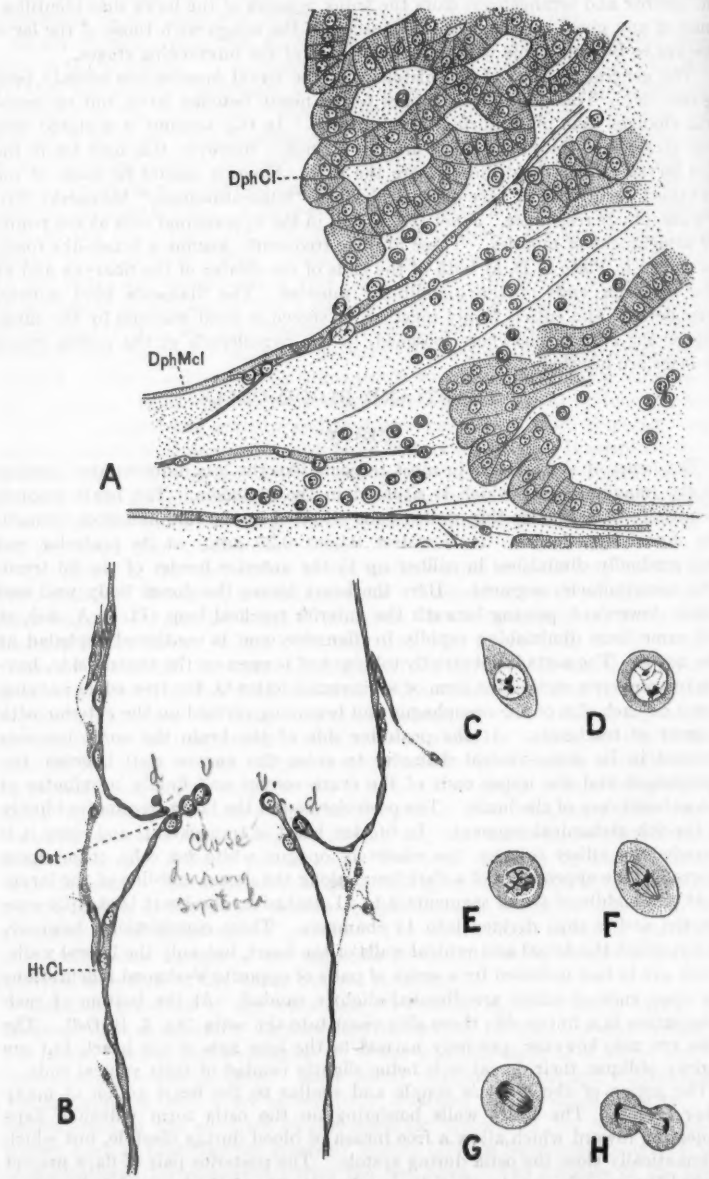

FIG. 5.—A, part of dorsal diaphragm of old larva, showing diaphragm cells (*Dph Cl*) and muscle fibers (*Dph Mcl*), ×66; B, longitudinal (coronal) section of heart in the region of the second thoracic segment, showing ostia (*Ost*) and valves. ×260; C—H, blood cells (lymphocytes), ×600

The wall of the heart is exceedingly thin, as shown by the figures, and is composed of a double row of cells, corresponding to the cardioblasts of the embryo, the two rows constituting the right and left sides of the heart, respectively. These cells have the form of the half of a radially compressed ring (Pl. 7, B). At the middle of its length each cell is thickened and at this point a large discoid nucleus is found. Traversing each of the heart cells lengthwise, that is, at right angles to the long axis of the heart and mesiad of the nucleus, is a bundle of delicate fibrils, few in number, usually visible only under high magnification. They are most readily seen in cross sections of the heart cells, that is, in longitudinal sections of the heart itself, which have been counterstained with eosin, the muscle fibrils of the heart cells, like those of other muscles in the larva, readily taking this stain. Their appearance in section is shown in figure 5, B, where they are represented in black. An attempt to represent these in lateral view is made in Plate 6, E, but they are actually less evident than here represented. In suitably stained preparations this bundle of fibers is plainly seen to be transversely striated (Pl. 6, F). The heart cells are therefore muscle cells, essentially similar structurally to other muscle cells in the bee larva, for example the trunk muscles, but in which the fibrillae (myofibrils) are more feebly developed. Similar conditions of structure are found in the cells of the heart wall of the larva of Tipula (*48*) and of those of Vespa (*1*) and Aeschna (*55*). Since the heart of all insects is contractile, it seems probable that further investigation will show such a differentiation to be general. In the larva of the honeybee, the myofibrils may easily escape notice, since larvae stained to show other structures to the best advantage scarcely show them at all. A deep and heavy stain with iron haematoxylin is necessary to reveal the myofibrils in face view; that is, in tangential sections of the heart. The arrangement of the heart cells in a double row is evidently not unique, since in addition to being characteristic of insect embryos it has been described for the Tipula larva by Viallanes and for the Aeschna larva by Zawarzin (*55*).

The heart is clothed externally by a loose meshwork of minute branched connective cells, the meshes tending toward elongation in a longitudinal direction (Pl. 6, E and F, *ConCls*). This meshwork serves to strengthen the heart wall and also to anchor the heart in position, since many of the processes of the connective tissue cells extend out to the hypodermis and to the adjacent fat cells.

DORSAL DIAPHRAGM

The dorsal diaphragm of the larva is well developed only in the posterior region, from the 4th to the 9th abdominal segments, inclusive, and here it is very similar in structure to that of the imago. In these segments it forms a continuous sheet, attached to the heart on its ventral surface (Pl. 7, A, B, *DDph*) and extending laterad, parallel with the dorsal body wall on either side of the dorsal midline, a distance somewhat less than one-eighth of the entire circumference of the larva. It partitions off a narrow dorsal space, the dorsal sinus or pericardial cavity. The lateral margins of the dorsal diaphragm are free except where they cross the lines of separation of the segments, and here the margins are attached to the body wall. Between these points the membrane is somewhat retracted mesiad, giving the margins a wavy contour (Pl. 7, A). The dorsal diaphragm terminates in the anterior half of the 9th abdominal segment with a free border. Anglas (*1*) states that the two delicate membranes ensheathing the diaphragm cells are reflected in the median plane below the heart to form a sort of septum which does not reach ventrad to the mid-intestine. This membrane, or septum, which is termed the "cloison médiane," is said to separate the fat body into two symmetrical halves. This account, as regards the bee larva, appears to be incor-

rect in several particulars. The "cloison médiane" is restricted to the anterior segments of the trunk; it does not form a continuous membrane; it does sometimes become attached to the muscular coat of the mid-intestine; it does not divide the fat body, since this is already divided mesially by a space or sinus dorsad to the mid-intestine; and it does not appear to be continuous with the two halves of the dorsal diaphragm, but represents delicate processes of connective tissue cells attached to the ventral surface of the heart. It is apparently absent in mature larvae and is probably a structure of minor importance.

Structurally the dorsal diaphragm consists of two very delicate membranes, having the appearance of basement membranes and possibly being chitinous. These membranes are attached to the ventral wall of the heart in the mid-line. Between the two membranes are situated the diaphragm cells (fig. 5, A, *DphCl*). These are small cells, quadrangular in form, each having a spherical nucleus which occupies the greater portion of the cell. The diaphragm cells are arranged in single rows or strings which are bent in a sinuous form and frequently anastomose, forming a sort of lacework and giving the dorsal diaphragm in surface view a curious vermiculated pattern (Pl. 7, A). These cells are not found anterior to the middle of the fourth abdominal segment. The diaphragm cells are closely covered on their dorsal and ventral faces by the two membranes, which here have the appearance of limiting membranes secreted by the cells (Pl. 7, B, *DDph*). Elsewhere, in the open spaces between the diaphragm cells, the two membranes are generally evident, but are often found in close apposition, giving the appearance of a single membrane.

The diaphragm cells have a general resemblance to the blood cells in size and staining reaction, and in the large size of the nucleus as compared with that of the cell body. For this reason Anglas (*1*) has assumed that the diaphragm cells give rise to blood cells (leucocytes). This may perhaps be possible, although the diaphragm cells are as a rule slightly larger than the blood cells. Moreover, the latter show such frequent mitoses that an independent origin for them need not be assumed.

Accompanying the dorsal diaphragm and forming an integral part of it are extremely delicate muscle fibers (fig. 5, A, *DphCl*), the so-called alary muscles, apparently unicellular and corresponding histologically to the fibrillae of other muscles. These fibers or fibrils are attached at more or less regular intervals to the ventral wall of the heart, the line of attachment coinciding with that of the membranes. The fibers corresponding to each chamber of the heart converge to their intersegmental points of attachment of the diaphragm on the body wall, thus giving the fibers the well known fan-like arrangement (Pl. 7, A). The relation of the diaphragm muscles to the membranes of the diaphragm does not seem to be uniform. At some points the muscles appear to run between the two membranes, at others dorsad to them. Thus far the description of the structure of the dorsal diaphragm of the larva corresponds with the account given by Snodgrass (*46*) for the imago. In the latter, however, the dorsal diaphragm terminates in the 7th abdominal segment, since the segments remaining are highly modified. The histological elements are the same in both, except that this structure in the imago is much more robust than in the larva, and can easily be seen on dissection, while in the larva it is so delicate that special methods are necessary to demonstrate it. In regard to one feature, a discrepancy exists between the two accounts. Snodgrass speaks of the diaphragm cells as situated upon the membrane, whereas in both cases they undoubtedly lie between two membranes.

The dorsal diaphragm anterior to abdominal segment 4 is less well defined than in the segments posterior to this point, and does not form a continuous sheet, being entirely absent in the middle of the segments and restricted to triangular areas corresponding with the diaphragm muscles (Pl. 7, A). These

areas naturally diminish in size with the diminishing size of the trunk segments. The whole of this anterior half of the dorsal diaphragm is, however, so exceedingly delicate that it is difficult to determine accurately its structure in detail. In preparations showing the dorsal diaphragm in surface view, such as that from which Plate 7, A, was taken, in the segments anterior to the 5th abdominal segment the dorsal diaphragm appears as a cobweblike structure in which only the radiating muscle fibers can be clearly discerned. In sections the muscle fibers may occasionally be found, and here and there are indications of an exceedingly fine structureless membrane; but the most conspicuous elements of the anterior half of the dorsal diaphragm are certain cells which may be called the anterior diaphragm cells. These are of relatively large size, and of pale appearance in stained preparations. The cytoplasm, besides being more transparent or less deeply stained, offers no peculiarities, and has a rather finely granular appearance. The nuclei are elliptical and, unlike those of the posterior diaphragm cells, are rather small as compared with the cytoplasm. In form these cells are irregular, although always flattened in a dorso-ventral direction. Their distribution is apparently scattered and irregular; some are found close to the heart wall, some at a considerable distance from it. Occasionally two or more are found associated together in small groups, attached end to end, but usually they occur singly. They never occur in long bands, as do the posterior diaphragm cells. Although they are frequently found crowded in among fat cells, it is usually possible to discern a connection with either the diaphragm muscles or the diaphragm membrane, if not with the heart itself.

The homology and function of these cells is unknown. On the basis of a study of the dorsal diaphragm, the writer (*36*), following Carrière and Bürger (*7*), thought that but two kinds of cells, exclusive of muscle cells, were found in the dorsal diaphragm; small epithelial cells, forming the major portion of the diaphragm, and a smaller number of large cells, assumed to be homologous with the "paracardial" cells found by Heymons (*14*) in certain Orthoptera. The conditions found in older larvae, as described above, make this view untenable. Definite information regarding the function and homologies of the two kinds of diaphragm cells in the larva of the honeybee will undoubtedly demand extended investigation.

VENTRAL DIAPHRAGM

The ventral diaphragm is well developed in newly-hatched larvae (*36*) and in the imago (*46*) and forms a continuous sheet made up of transversely arranged muscle fibers overarching the ventral nerve cord and partitioning off a ventral (perineural) sinus. In older larvae it becomes merely a vestigial structure confined to the abdominal segments, and composed of more or less isolated delicate muscle fibers crossing the body cavity above the ventral nerve cord. They are entirely too few in number to form anything even approaching a membrane in structure, and constitute only a very loose and insignificant meshwork (Pl. 5, A, *VDph*).

BLOOD

The blood comprises a transparent fluid, the plasma, watery and only slightly viscid, and the blood cells (blood corpuscles, leucocytes) or amoebocytes. In the feeding larva the latter are of one sort only and correspond to the young amoebocytes of Cuénot (*8*). The amoebocytes of the bee larva are scattered throughout the spaces filled by the blood, but are usually more numerous in the dorsal sinus in the region of the heart. They vary in form from ovoid or ellipsoid to spherical, but the latter form is assumed only by cells preparing to divide. The ovoid form (fig. 5, C) is the one most frequently assumed by resting amoebocytes. In narrow spaces these are sometimes found slightly deformed by

pressure from the adjoining tissues, but no evidence of a true amoeboid movement was observed. Unlike the cells of many other organs and tissues of the larva, such as those of the mid-intestine and of the fat body, the size of the amoebocytes remains nearly constant throughout the life of the larva, and is from 6 to 9 microns wide and 7 to 12 microns long. The cytoplasm stains moderately with the usual chromatin stains and normally presents no evident differentiations or inclusions. The nucleus is relatively very large, is spherical in form, and contains a few small chromatin granules. Cells in mitosis are quite frequent (fig. 5, D–H) and it is easy to find a series representing the different phases. This seems to be the normal if not the only mode of increase, since there is no good evidence of a special blood-forming tissue in the bee larva.

Anglas (*1*) describes a second type of blood cell "lymphocyte," larger, and with the cytoplasm finely vacuolated. This type apparently does not appear in the larva prior to capping.

The action of the heart and the flow of the blood are very similar to those of the imago, as described by Snodgrass (*46*), except that the sole propulsive organ is the heart. Except in very young larvae, the ventral diaphragm is so poorly developed that its action must be practically negligible. In a mature living larva, removed from the cell, successive waves of contraction are seen to pass cephalad over the heart at the rate of about one per second at room temperature, driving the blood into the head cavity. From here the blood flows caudad, filtering back through the channels formed by the various spaces between the fat body and the viscera. Some of these spaces are sufficiently well defined to deserve to be called blood sinuses. The most conspicuous of these is the ventral sinus (Pl. 5, A, *VS*), a tubular space extending the entire length of the larva above the ventral nerve cord and bounded laterally and dorsally by lobes of the fat body. As the figure shows, it is not limited dorsally by the ventral diaphragm (*VDph*), as it is in other insects. Another considerable space is found between the heart and the alimentary canal, while a continuous space exists around the mid-intestine, permitting a free flow of blood over the external face of the latter. Around the tracheal trunks and their principal branches are also narrow spaces free from fat cells, which form blood channels. The pericardial chamber is more or less completely filled with fat cells (the pericardial fat cells) except in the middle of each segment, where there is a space on each side of the heart, opposite the ostia, which is unoccupied by fat cells. These spaces extend laterad from the heart a short distance, and each receives one of the dorsal tracheal branches (fig. 2, A), being thus connected with the blood channel accompanying this branch. In the living larva blood may be seen flowing dorsad along this path. The pericardial blood lacuna just described may be seen in Plate 7, A, in which the round pericardial cells are represented in dotted outline. It should be stated, however, that these cells actually extend farther laterad than is shown, many of them having been removed in dissection. In the living larvae, and even in some fixed specimens, these pericardial lacunae are evident externally as short dark bands extending right and left from the heart in each segment (see Pl. 1, E).

FAT CELLS, OENOCYTES, EXCRETORY CELLS

FAT CELLS

At all stages except the earliest, fat cells, constituting collectively the so-called fat body, occupy approximately a half of the body cavity not already occupied by the other viscera. In life the fat cells are nearly opaque and colorless. Since they underlie the transparent hypodermis over the greater portion of the body they are largely responsible for the ivory-white tint of the larva. In general, the fat cells adhere together in flat lobular masses or strings, supported by tracheae

and projecting centrad into the body cavity (Pl. 5, A, *1–3F*). In the arrangement of these masses a certain amount of bilateral symmetry exists. Carrière and Bürger (*7*), in their description of the larval mason bee, divide the fat body into three sections: (1) That part, situated dorsad to the lateral tracheal trunks and below the dorsal diaphragm (Pl. 5 A, *1F*); (2) that part situated ventrad to the lateral tracheal trunks (*2F*); (3) that part situated above the dorsal diaphragm and comprising one to three layers of cells (*3F*). These divisions are only incompletely separated and are merely of topographic value, since there are no differences in the morphological character of the cells themselves. As shown in Plate 5, A, the fat cells are most abundant peripherally, next to the body wall, a considerable space around the alimentary canal being left vacant (see p. 1184). In advanced larvae fat cells are abundantly present in contact with the hypodermis, but not attached to it, throughout the trunk, crowded between the hypodermis and muscles and also beneath the ventral nerve cord. A few fat cells are likewise present in the head, lying against the posterior surface of the brain and below the suboesophageal ganglion. The various open spaces in the fat body, constituting channels for the flow of blood, have been described in a previous section (see p. 1199).

Bishop (*4*) has published a detailed account of the structure and development of the fat cells of the honeybee larva, to which the reader is referred for more extended information on this subject. In quite young larvae the deutoplasm of the fat cells (Pl. 8, D and E, *F*) is commonly found represented in each cell by a single relatively large vacuole (*y*), while the nucleus is still more or less spherical. In larvae three to four days old the deutoplasm of the fat cells (Pl. 8, F, *y*) is scattered throughout the cytoplasm in the form of vacuoles of various sizes; at the same time the nuclei begin to show distortion. Plate 8 illustrates a typical fat cell (*F*) from a mature larva, in which the nucleus has assumed the shrunken and branching form characteristic of this stage.

OENOCYTES

The oenocytes of the honeybee have been described by Wielowieysky (*52*), Koschevnikov (*27*), Anglas (*1*), and the writer (*36*). They are very conspicuous in sections, on account both of their large size and their great affinity for stains. They are rare in the thoracic segments, but are found abundantly throughout the abdomen, always occurring singly, never in groups, and generally, if not invariably, in more or less intimate contact with fat cells. In mature larvae the oenocytes closely approximate the fat cells in size, but this is not true of younger larvae. In a larva two days old, for example, the average diameter of the oenocytes is about twice that of the fat cells (Pl. 8, D, *Oen*). The rate of growth of the fat cells therefore greatly exceeds that of the oenocytes. Generally speaking, the oencytes are more or less ellipsoid in form, but modifications of this are frequent and of such a kind as to afford plain evidence of the amoeboid, wandering nature of these cells. The oenocyte represented in Plate 8, *B*, is deformed to accommodate itself not only to the two adjacent fat cells (*F*, *F*) but also to a blood cell (*BlC*). It is to be noted that the contour of the fat cells is not evidently altered. Many oenocytes are found with a pointed process at one end—evidently a pseudopodium—extending between the adjacent fat cells, as though wedging them apart, while other oenocytes possess two such processes which are applied to and partially surround one or more of the adjacent fat cells. One instance of the amoeboid character of the oenocytes, as seen in sections, was particularly striking; here an oenocyte had assumed the form of a crescent embracing a fat cell between its horns, thus irresistibly suggesting the movements of an amoeba preliminary to ingesting its prey. The oenocytes, however, never

contain food vacuoles, nor do they in fact give any good evidence of being phagocytic in character. This is in accord with the observations of Anglas (*1*) on the wasp and honeybee and Pérez (*40*) on the ant.

The nuclei of the oenocytes are spherical or ellipsoid and contain a large number of subequal chromatin granules uniformly distributed (Pl. 8, B, *Oen*). The cytoplasm is dense, staining intensely in both haematoxylin and eosin, and exhibits variations in density which give it a characteristic mottled or marbled appearance.

EXCRETORY OR URATE CELLS

In the mature larva of the honeybee these cells, as stated by Anglas, occur only in small number. They are found in the abdomen, interpolated singly here and there among the fat cells, with which they are always closely associated. As shown in Plate 8, C, *u*, they are cells of somewhat irregular form, having a diameter about half that of the fat cells. The nucleus is spherical and contains a relatively scanty amount of chromatin in the form of small granules. The cytoplasm has a fine and regular alveolar structure, and in sections usually appears pale, having slight affinity for stains. In a very young larva (two days old) the excretory cells (Pl. 8, D, *u*) appear to be more numerous than in older larvae, and may be found in groups or clusters. They are here rendered more conspicuous both by their relatively greater size, which is equal to that of the fat cells, and more particularly by the greenish-yellow color of their cytoplasm. Under high magnification (1/12 homo. immers.) minute refractive greenish particles may be seen within the alveoles.

The general resemblance of the excretory cells to the fat cells and their close association with them at this stage argues strongly for a community of origin, as assumed by both Pérez (*40*) for the ant and Anglas (*1*) for the wasp and bee. Berlese (*3*) suggests that the excretory cells and the oencocytes have had a common origin. In Plate 8, D, an oenocyte from the same section as the other cells is introduced for comparison. The discrepancy in size and in other characters between this cell on the one hand and the fat and excretory cells on the other is sufficiently obvious. Moreover, the oenocytes are well differentiated and possess most of their distinctive characters even at the time of hatching (*36*).

RUDIMENTS OF GONADS

OVARIES

In the mature worker larva the ovarian rudiments are two small flat structures, one situtated on either side of the dorsal mid-line in the 5th abdominal segment (Pl. 8, G, *Ov.*). In side view each of these rudiments (Pl. 8, I) presents a trapezoidal outline, the dorsal and ventral margins being parallel, while the two ends are abruptly narrowed to form slender tapering filamentous processes which extend cephalad and caudad along the ventral side of the heart into the 4th and 6th abdominal segments respectively. Exclusive of these processes, the length of the rudiment does not exceed half of that of the segment in which it lies. The ventral margin is thickened, the dorsal margin thin, so that in section each rudiment presents a pyriform outline (Pl. 8, G and H, *Ov.*).

Histologically each rudiment is composed principally of a close network of minute branching connective tissue cells (Pl. 8, H) enclosed by an epithelium made up of minute flat cells and covered externally by a cuticular tunic. From the dorsal border delicate cell-strands, clothed with a membrane continuous with the tunic, pass to the ventral wall of the heart on either side of the mid-line, thus acting as suspensory ligaments. The dorsal borders of the rudiments lie close to the mid-line, but their ventral borders lie farther apart, so that the mesial surfaces

of the rudiments are inclined at an angle of about 45 degrees to the median plane (Pl. 8, G, *Ov.*). The ventral half of each rudiment is traversed at right angles to its long axis by a large number of slender parallel columns or strings of cells with deeply stained cytoplasm, each column consisting of several rows of such cells (Pl. 8, H). These columns are assumed to be the rudiments of the ovarian tubules of the imaginal ovary. Their ventral ends extend to the ventral borders of the ovarian rudiments; the spaces between them are filled with branched connective tissue cells.

Along the ventral margin of each ovarian rudiment is a groove, at the bottom of which is located a ridge (Pl. 8, H, *Ovd*) composed of minute vacuolated cells. The base of this ridge is closely associated with the ventral or distal ends of the ovarian tubules. Near the posterior end of the rudiment the ridge becomes separated off as a solid cord of cells, taking a ventrad and caudad direction (Pl. 8, I and K, *OvD*), evidently becoming the rudiment of the oviduct.

Numerous tracheoles are found within the connective-tissue matrix surrounding the ovarian tubules. In some cases end cells have been observed within the rudiments of the ovaries.

In a mature larva, reared in a queen cell, the rudiments of the ovaries are long reniform structures (Pl. 8, L, *Ov*). measuring about 2.25 mm. in length and attached to the ventral wall of the heart in the 5th abdominal segment. The anterior ends of these rudiments, which lie on the boundary between the 4th and 5th abdominal segments, are each prolonged to form slender pointed processes like those found in the worker larva. With the exception of these insignificant processes the entire ovarian rudiment of the queen larva is composed of transverse parallel columns of dark-staining cells, assumed to represent the future ovarian tubules, similar to those of the worker larva but far more numerous, of larger diameter, and extending from the ventral to the dorsal margin. These are of course united by a connective tissue network. The (presumptive) rudiments of the oviducts are similar to those of the worker larva.

TESTES

These are relatively enormous structures, measuring about 3.75 mm. in length and 1.25 mm. in breadth, and lie on either side of the heart in the 4th, 5th and 6th abdominal segments, close to the dorsal body wall. They are elongate reniform in outline (Pl. 8, J, *Tes*) and somewhat compressed in a dorso-ventral direction. Like the ovarian rudiments, those of the testes are made up of numerous parallel transverse cell strands bound together by connective tissue. The (presumptive) rudiments of the vasa diferentia (*VDef*) are similar to those of the oviducts in the worker and queen larvae, but more delicate and more difficult to demonstrate.

TECHNIQUE

Several fixing fluids were tried for killing and fixing bee larvae, but none gave as general satisfaction as Carnoy's acetic-alcohol mixtures. Their success is largely due to their superior power of penetration, since the chitinous cuticle of the larva, although very thin and delicate, is almost impenetrable by aqueous solutions.

The study of the internal organs by dissection is made difficult by the short and curved form of the larva, its small size, the abundance of fat cells and the general delicacy of the tissues. The preparation represented by Plate 4, A, was made from a larva fixed in Carnoy's fluid, stained over night in Mayer's carmalum and heavily destained (4 to 6 hours) in acidulated alcohol. The body wall, muscles, coagulated blood, etc., were then removed bit by bit with a needle, the stain rendering possible the identification of the different organs and tissues.

This method of dissection was the one usually employed. Fresh material was not found satisfactory. Very successful entire preparations of separate parts, such as the head, were made by staining for 18 to 24 hours in carmalum and afterwards destaining in acidulated alcohol (0.1 per cent) for about the same length of time. To demonstrate the dorsal diaphragm, the larva was first killed and the body wall and muscles fixed by immersion in absolute alcohol for five minutes. The dorsal body wall was then removed with the aid of fine scissors, spread out on a slide, ventral surface uppermost, and the fat body gently pushed away from either side of the dorsal mid-line, thus uncovering the dorsal diaphragm. The latter was then fixed with any convenient fixing fluid, stained rapidly (5 minutes) with Ehrlich's haematoxylin, dehydrated, cleared, and mounted, together with the dorsal body wall, to which it remains attached.

Sections were made in the usual manner. Celloidin sections 30 to 40 microns thick were found very useful in determining the relation and size of organs. Sections of material imbedded in paraffin were cut 6 to 8 microns in thickness, since the completeness of the series was usually more important than extreme thinness of individual sections. Prior to embedding, the larvae were either cut in half, or, when sagittal sections were desired, an aperture of considerable size was made in the lateral body wall. Infiltration is complete in 4 to 6 hours, if xylol has been used for clearing.

Iron haematoxylin proved to be the only satisfactory stain for sections of material embedded in paraffin, the other haematoxylin stains being too diffuse in their action. A counter stain such as Orange G or alcoholic solution of eosin is useful in differentiating certain structures, such as nerve fibers or the albuminoid granules of the fat cells. Material intended for celloidin sections was stained in bulk with Mayer's carmalum.

SUMMARY

(1) The bee larva has a fusiform shape, the posterior end being the smaller, and is flexed ventrad. Its color is ivory white. The larva is divided by constrictions into a head and 13 segments, 3 of which belong to the thorax, the remainder to the abdomen. The sternal surface of the abdomen is sharply demarcated from the lateral surfaces by the ventrolateral suture. The ventrolateral region of abdominal segments 1 to 9 is raised to form a series of rounded swellings, the epipleural lobes.

Ten pairs of spiracles are present, situated on the lateral faces of the 1st and 2d thoracic and the first eight abdominal segments, near their anterior limits. The head is short and blunt and the neck constriction is a narrow fold. The labium is prominent, bluntly conical, slightly compressed dorso-ventrally, and bears on its tip the common opening of the silk glands. The maxillae and mandibles are papillate, the mandibles being more pointed than the maxillae and curved mesiad. A well-defined groove, the lateral furrow, runs from between the bases of the mandibles and maxillae caudad to the neck constriction. The labrum is broad and flat, slightly bilobed at its apex, and is indistinctly marked off from the clypeus. The labrum and labium are separated by a narrow cleft-like space, the mouth opening, which is bounded laterally by the mandibles and maxillae. On each side of the clypeus the antennal rudiments are evident as circular papillate elevations.

(2) The body wall consists of a single epithelial layer of small cells, the hypodermis, clothed externally by a delicate cuticle. The hypodermis differs greatly in thickness in different parts of the body but its average thickness is greatest in the head. The cuticle also is here thicker and more rigid than elsewhere. The antennal rudiments are ovoid in form and situated in deep peripodal cavities,

only the peripheral ends of the rudiments projecting above the surface of the head. The peripodal cavities of the antennae as well as of the other appendages are closed externally only by cuticle. The wing rudiments are small, flat, heart-shaped, hollow outgrowths of the hypodermis situated in shallow depressions low down on the second and third thoracic segments. The leg rudiments are ovoid in shape and are situated in deep peripodal cavities on the ventral side of the three thoracic segments, close to the mid-line. The genital rudiments are six in number, one pair being situated on the 8th abdominal segment and the other two pairs on the 9th. They are knob-like in form and lie in shallow open depressions.

(3) The rigidity of the head capsule is increased by the tentorium, which consists of a system of tubular ingrowths of the hypodermis lined by chitin. It comprises two short and broad posterior arms which are attached to the cranial wall at the junction of the lateral furrows with the neck fold; a transverse central body, continuous with the lateral arms; and two slender anterior arms joining the ends of the central body to the cranial wall at the sides of the clypeus. On the lateral face of each of the anterior arms is a spine for the attachment of a muscle. At the base of each of the mandibles, on its mesial side, is a hollow spine-like apodeme for the insertion of the adductor muscle.

(4) The nervous system is simple and primitive as compared with that of the adult and consists, in the mature larva, of a brain, a nerve chain comprising 11 ganglia joined by paired connectives and a stomatogastric ganglion with its accompanying nerves. The brain includes a pair of large somewhat crescentic or auriculate optic lobes, situated in the transverse plane, well-developed protocerebral lobes, and small antennal lobes (deutocerebrum) and tritocerebral lobes. The two halves of the latter are united by a distinct suboesophageal commissure which is not fused with the suboesophageal ganglion. Two pairs of nerves spring from the brain proper: the antennal nerves, which connect the antennal lobes with the antennal rudiments, and the labrofrontal nerves, which spring from the tritocerebral lobes. Each of these last mentioned nerves divides near its point of origin into the frontal nerve, which runs mesiad to the frontal ganglion, and the labral nerve, which innervates the labrum. The suboesophageal ganglion, attached to the brain by slender crura cerebri, is somewhat lenticular in form, broader at its anterior end. It represents three pairs of simple ganglia and gives rise on each side to four nerves: mandibular, maxillary, labial, and the X-nerve of Jonescu. The last mentioned possibly corresponds to the salivary gland nerve in other insects. In the bee larva it is difficult to trace but appears to terminate in the superficial hypodermis at the base of the labium. The 11 ganglia of the ventral cord are lenticular in form and are connected with one another by distinct parallel connectives. The ganglia are not located in the middle of the segments but are near their anterior ends. The three thoracic ganglia are the largest, those of the following seven abdominal segments being subequal; the 8th abdominal ganglion is, however, elongate and comprises three pairs of simple ganglia and the rudiment of a fourth. All of the abdominal ganglia are provided with well-developed lateral nerves which divide into branches supplying the viscera, muscles, etc. The stomatogastric system comprises a well-developed stomatogastric ganglion situated above the pharynx and connected to the brain by the frontal nerves. Anteriorly it gives off a single nerve, the superior pharyngeal nerve, supplying the superior pharyngeal muscles and the tip of the labrum. Posteriorly the stomatogastric ganglion gives off a stout nerve which passes caudad, diminishing in caliber meanwhile, along the dorsal surface of the oesophagus. It finally breaks up into small branches.

The nervous system of the larva is histologically similar to that of the imago but is of course less specialized. The central nervous system displays the usual

division into an outer and cortical zone of ganglion cells surrounding an inner central core of nerve fibers (punk-substanz). Among the ganglion cells large actively dividing neuroblasts, like those of embryos, may frequently be recognized. An outer neurilemma is always distinguishable; an inner neurilemma is probably also constantly present, but less evident. In the brain of the larva many of the typical features of the imaginal brain may be readily recognized, such as the arrangement of the cells of the optic lobes to form inner, middle and outer fibrillar masses, and the presence of well-developed mushroom bodies.

(5) The corpora allata are spherical bodies about 0.85 mm. in diameter, situated one on each side of the mid-line, close behind the brain, lying on the dorsal side of the anterior arms of the tentorium, and in close contact with the walls of the aorta. Each is composed of a compact mass of polyhedral cells. Tracheoles may be seen to enter these bodies and penetrate between their component cells.

(6) There are ten pairs of spiracles, following the rule for insect larvae, located on the 2d and 3d thoracic and the first eight abdominal segments. The spiracles of each side open by short branches into a longitudinal trunk. The two trunks are united anteriorly by a loop or commissure in the region of the neck, above the oesophagus, and posteriorly by a similar loop below the hind-intestine. The longitudinal trunks are also connected by segmentally arranged commissures which run close to the ventral body wall. Two pairs of tracheal branches from the anterior tracheal loop supply the brain, antennal rudiments and other parts of the head. Segmentally arranged branches springing from the longitudinal tracheal trunks supply the muscles, heart and viscera. The tracheae terminate in typical tracheal end cells from which arise the tracheoles. The latter never branch or anastomose and have never been observed to penetrate the cytoplasm of other cells.

(7) The alimentary canal comprises a short and relatively slender fore-intestine, a large cylindrical mid-intestine and a hind-intestine. The fore-intestine includes mouth, pharynx and oesophagus, these three divisions being somewhat ill-defined. The mouth is a wide transverse slit passing immediately into the pharynx. The latter is provided with a well-developed epipharynx which consists essentially of a fold of the dorsal wall of the pharynx, and which is provided with numerous transversely arranged muscles uniting the lateral margins of the fold and also with levator muscles which are attached at the dorsal ends to the dorsal wall of the clypeus and labrum. In addition, the pharynx itself is provided with two sets of dilator muscles and a pair of levators. The pharynx leads directly into the tubular oesophagus, which opens into the anterior end of the mid-intestine. Here the wall of the oesophagus is reflected upon itself to form a fold which projects into the anterior end of the mid-intestine, thus constituting an oesophageal valve similar to that found in many other insects. The oesophagus is provided with a muscular coat composed mainly of transverse fibers. The mid-intestine is very capacious, cylindrical in form, about one-third of the diameter of the body and extends from the prothoracic to the 9th abdominal segment. Its walls are thick and composed of large cubical cells displaying the usual striated border. A peritrophic membrane, apparently gelatinous in consistency, lines the mid-intestine. This layer appears to be secreted by those cells of the mid-intestine lying next to the oesophageal valve. The mid-intestine possesses a muscular coat composed of an inner layer of delicate longitudinal fibers and an outer layer of transverse fibers. The muscle fibers of both layers are branched and anastomose with one another. This is more conspicuously seen, however, in the case of the inner longitudinal layer. The posterior end of the mid-intestine is completely closed and its extremity is not covered by the muscular coat. The hind-intestine is a relatively slender tube, doubled on itself

and of uniform diameter except at its anterior end, which is enlarged and closed anteriorly by a thin diaphragm-like membrane which is closely applied to the extreme posterior end of the mid-intestine. The hind-intestine is clothed with a well-developed muscular coat composed of an inner layer of circular (transverse) muscle fibers and an outer layer of longitudinal fibers. Posteriorly the hind-intestine terminates in a slit-like anus. Here the hind-intestine is provided with muscle fibers which act as dilators.

(8) The Malpighian tubules are long and winding, extending cephalad to the region of the metathorax. Their tapering and pointed posterior (central) ends are blind and are inserted between the posterior extremity of the mid-intestine and the thin epithelial layer closing the anterior end of the hind-intestine. In young larvae the Malpighian tubules are slender, with a small lumen and relatively thick walls; in old larvae they attain a relatively large diameter and possess very thin walls, being obviously much distended. After the cell occupied by the larva has been sealed and communication between the mid- and hind-intestine has been established, permitting the discharge of feces, each of the Malpighian tubules acquires an opening into the mid-intestine by means of a minute canal perforating the annular remains of the epithelial layer which formerly closed the anterior end of the hind-intestine. The discharge of the fluid excreta of the Malpighian tubules thus occurs simultaneously with the discharge of solid excreta from the mid- and hind-intestines.

(9) The silk glands comprise a pair of slender tubes, thrown into numerous short convolutions and extending nearly the entire length of the larva, below the mid-intestine. Their anterior ends unite to form a thin-walled duct, lined with chitin, which opens by a slit-like aperture on an elevation situated on the tip of the labium.

(10) The trunk muscles are the same in all the abdominal segments except the 10th, and are (1) ventral longitudinal, a group occupying the sternal region of each segment and connecting its anterior and posterior margins; (2) ventral oblique, a pair of flat bands running obliquely cephalad and mesiad across the sternal region and also connecting the anterior and posterior margins of each segment; (3) lateral oblique, comprising one stout band crossing the lateral region of each segment in a cephalad and mesiad direction and connecting the two margins of the segment, and a small band crossing the lateral region in the opposite direction and having its dorsal end attached to the body wall in the region of the spiracle; (4) two small dorso-ventral bands; (5) dorsal longitudinal muscles connecting the anterior and posterior dorsal margins of the segments; (6) dorsal oblique muscles running from the posterior margin of each segment, in the dorso-lateral region, obliquely cephalad and mesiad to an oblique line of attachment on the body wall, the sutural line separating the prescutum and the scutoscutellum. Since the body wall is nowhere rigid, the arrangement of the muscles is responsible, to a large extent at least, for the external contour of the larva.

(11) The heart is a thin-walled tube, blind at its posterior end and running the entire length of the body in the mid-line close to the dorsal body wall, and continuous cephalad as the aorta, which enters the head. The structure of the larval heart closely resembles that part of the imaginal heart lying in the abdomen. It posses a pair of valvular ostia in every segment except the 1st (possibly also the 2d) thoracic segment and the 9th and 10th abdominal segments. The heart is composed of two rows of flat cells on each side of the mid-line. The cytoplasm of these cells is differentiated to form striped muscle fibers. Externally the heart is clothed with a network of branching minute connective tissue cells. A dorsal diaphragm is present which is especially well-developed in the 4th to the 9th abdominal segments, where it is composed largely of sinuous bands of small

cells, as in the adult. Anterior to this region a few cells of medium size, of unknown significance, are found attached to the ventral border of the heart. The ventral diaphragm is well developed in young larvae, consisting of a sheet formed of transverse muscle fibers, spanning the lower portion of the body cavity. In old larvae, however, there remain only a few scattered muscle cells. The blood cells of the larva are all of one kind, of minute size and ellipsoid form. Many are found in division, indicating that this is the chief, if not the only, method of increase, since no blood-forming tissue is found.

(12) The fat body is voluminous, occupying a large part of the body cavity. Certain spaces are, however, left open for the flow of blood. The most evident of these are, (1) a tubular space extending longitudinally beneath the alimentary canal; (2) an annular space around the mid-intestine; (3) a tubular space extending longitudinally above the alimentary canal; (4) a set of transverse spaces in the dorsal region of the body, one in the middle of each segment and communicating with the ostia of the heart. Excretory (urate) cells are present in limited number, scattered among the fat cells. Oenocytes are very abundant and conspicuous because of their large size and staining reaction. They are found scattered throughout the trunk, but are most abundant in the abdomen. They are evidently amoeboid wandering cells, but no evidence of phagocytic activities was found.

(13) The rudiments of ovaries in the worker larvae are very small and situated in the 5th abdominal segment, attached to the ventral border of the heart and consisting principally of connective tissue, in which are embedded transverse strands of minute cells. These strands are presumably rudiments of ovarian tubes. Rudiments of oviducts are present as delicate solid strands of cells. The rudiments of ovaries in the queen larva are much larger than in the worker larva, showing that their development is greatly accelerated during the later larval stages. Their structure is similar to that of the worker larva except that the presumptive rudiments of ovarian tubes are both more numerous and longer. The rudiments of testes in the drone larva are relatively enormous, lying in the 4th, 5th and 6th abdominal segments, and are composed of very numerous transversely arranged strands of cells united by connective tissue. Rudiments of vasa deferentia are present.

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EXPLANATION OF SYMBOLS USED IN PLATES AND TEXT FIGURES

AntL, Antennal lobe.
AntNv, Antennal nerve.
Ant, Antennal rudiment.
Ao, Aorta.
ApTen, Spur on anterior arms of tentorium.
ATraL, Anterior tracheal loop.
BlC, Blood cells.
Br, Brain.
1Br, Protocerebral lobes.
3Br, Tritocerebral lobes.
Bra1, *Bra2*, Tracheal branches to head.
CCer, Crura cerebri.
Clp, Clypeus.
Com, Commissure of ventral nerve cord.
Con, Connective of ventral nerve cord.
ConCls, Connective tissue cells.
CorAll, corpora allata.
Cu, Cuticle.
DDph, Dorsal diaphragm.
DilPhy, dilator muscles of pharynx.
DLMcl, Dorsal longitudinal muscles.
DOMcl, Dorsal oblique muscles of trunk.
dph, Diaphragm closing anterior end of hind intestine.
DphCl, Diaphragm cells of heart.
DphMcl, Muscle fibers of dorsal diaphragm.
EMd, Extensor muscle of mandible.
EMx, Extensor muscle of maxilla.
EpL, Epipleural lobes.
Ephy, Epipharynx.
EphyMcl, Epipharyngeal muscles.
1F–3F, Fat cells.
f, Fatty globules of fat cells.
fm1, Outer fibrillar mass of optic ganglion.
fm2, Middle fibrillar mass of optic ganglion.
fm3, Inner fibrillar mass of optic ganglion.
FtGng, Frontal ganglion.
FtNv, Frontal nerve.
1G–3G, First second, and third pairs of genital rudiments.
Gng, Ganglion.
HInt, Hind intestine.
Ht, Heart.
HtCl, *HtCls*, Pericardial cell, pericardial cells.
Hyp, Hypodermis.
Hphy, Hypopharynx.
ImCls, Imaginal cells of mid intestine.
INlm, Inner neurilemma.
In, Intima.
1L, *2L*, *3L*, Thoracic legs (rudiments).
Lb, Labium.
LbNv, Labial nerve.
LevEphy, Levator muscle of epipharynx.
LevPhy, Levator muscle of pharynx.
Lm, Labrum.
LMcl, Longitudinal muscles of alimentary canal.
LmNv, Labrofrontal nerve.
LNv, Lateral nerve.
LNvF, Lateral nerve fibers.
1LOMcl, Major lateral oblique muscles of trunk.
2LOMcl, Minor lateral oblique muscles of trunk.
Mal, Malppighian tubules of larva.
mal, Malpighian tubules of imago.
MB, Mushroom bodies.
MclEnt, Muscular layer of alimentary canal.

Md, Mandible.
MdNv, Mandibular nerve.
MInt, Mid intestine.
Mth, Mouth.
Mx, Maxilla.
MxNv, Maxillary nerve.
Nbl, Neuroblasts.
Nlm, Neurilemma (outer).
Nu, Nucleus.
NvF, Nerve fibers.
O, rudiment of ocellus.
Oe, Oesophagus.
OeCom, Circumoesophageal commissure.
Oen, Oenocyte.
OeVlv, Oesophageal (proventricular) valve.
OpL, Optic lobe.
OpPl, Optic plate.
Ost, Ostia of heart.
Ov, Ovary.
OvD, Oviduct.
Pmb, Peritrophic membrane.
PrF, Postretinal fibers.
Prs, Prescutal area.
PTraL, Posterior tracheal loop.
qq, Food matter in mid intestine.
RAp, Retractor apodeme of mandible.
1RLb, Major retractor muscle of labium.
2RLb, Minor retractor muscle of labium.
RMd, Retractor (adductor) muscle of mandible.
RMx, Retractor muscle of maxilla.
Scs, Scuto-scutellar area.
SDilPhy, Superior dilator muscles of pharynx.
SlkD, Common duct of silk glands.
SlkDO, External opening of common duct of silk glands.
SlkGl, Silk glands.
SoeCom, Suboesophageal commissure.
SoeGng, Suboesophageal ganglion.
Sp, Spiracle.
SpBr, Tracheal branch to spiracle.
SPhyNv, Superior pharyngeal nerve.
st, Stalk, or projection of fundus of midintestine.
StgNv, Stomatogastric nerve.
StrBor, Striated border of the epithelium of the midintestine.
SupCom, Supraoesophageal commissure.
Ten, Central body of tentorium.
1Ten, *2Ten*, Anterior and posterior arms of tentorium.
Tes, Testis.
TMcl, Transverse muscles of alimentary canal.
Tra, Trachea.
tra, Tracheoles.
TraCom, Tracheal commissure.
TraECl, Tracheal end cell.
TraTr, Tracheal trunk.
U, Urate or excretory cell.
VDef, Vas deferens.
VDph, Ventral diaphragm.
VLMcl, Ventral longitudinal muscles.
VlS, Ventrolateral suture.
VNC, Ventral nerve cord.
VOMcl, Ventral oblique muscles of trunk.
VS, Ventral sinus.
WngR, Rudiments of wings.
X, Nerve designated as "X" by Jonescu.
y, Food reserve in fat cells.

PLATE 1

Larva of the honeybee

A.—Head of mature larva, treated with caustic potash, showing endoskeleton, viewed from dorsal surface. × 26.

B.—Brain and suboesophageal ganglion of mature larva, face view. Drawn from a wax model reconstructed from sections and verified by dissections. × 40.

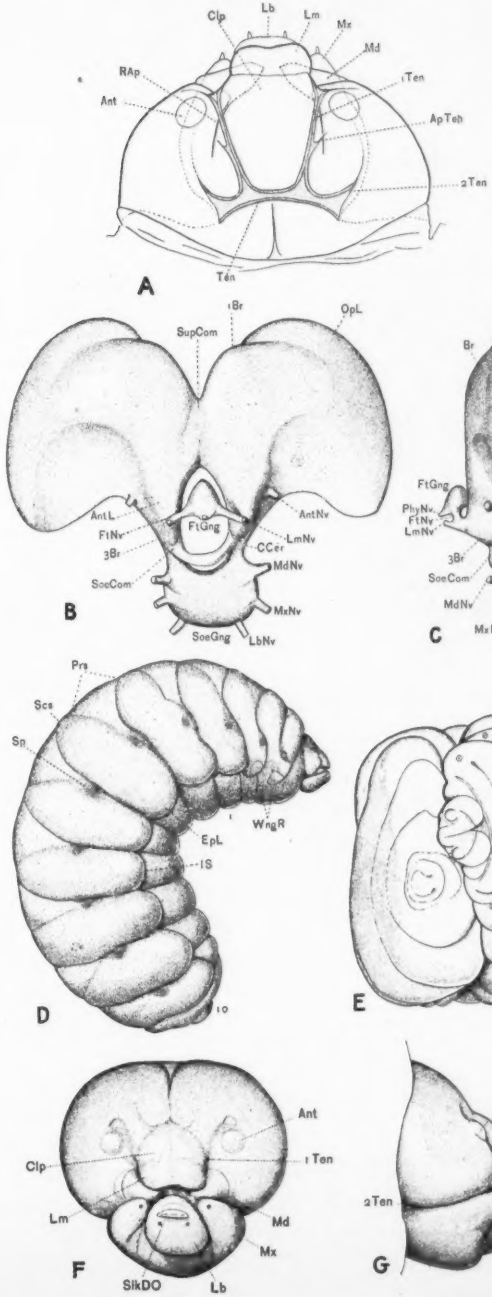
C.—Same as B, side view. × 40.

D.—Mature worker larva, removed from cell, viewed from the right side. × 6.

E.—Mature worker larva, fixed within the cell and afterwards removed, showing the compressed hexagonal form assumed while within the cell. The head and anus are both turned toward the observer, the body being bent in the shape of the letter U. × 6.

F.—Face view of head of mature larva. × 20.

G.—Head of mature larva, side view. × 20.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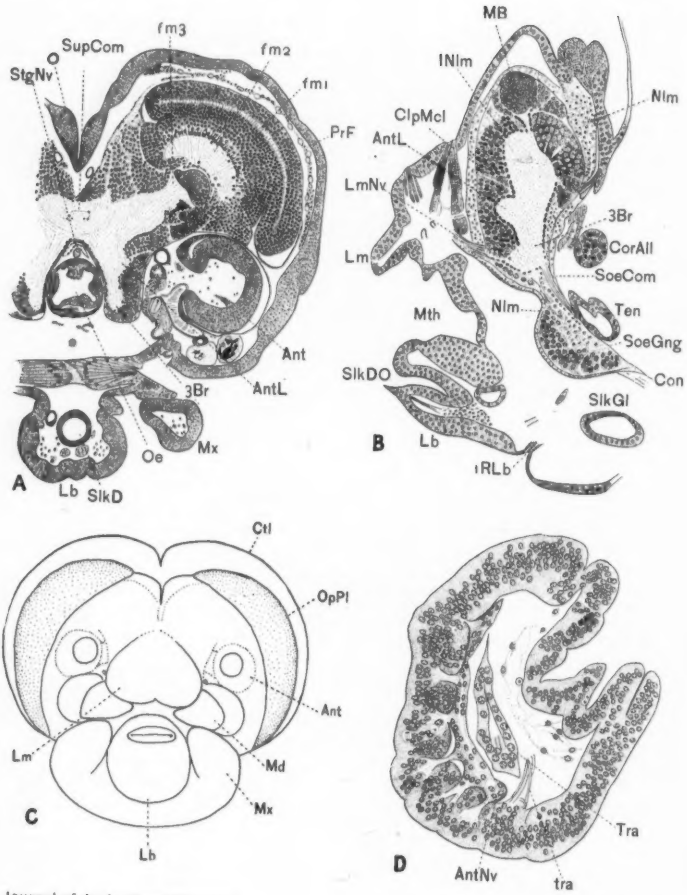
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PLATE 2

Larva of the honeybee

A.—Cross section of head of mature larva, intersecting the optic lobes (*fm 1-3*) and antennal lobes (*AntL*). × 60.

B.—Longitudinal section of head of mature larva, passing through one of the suboesophageal commissures (*SoeCom*). × 60.

C.—Head of larva, face view, showing the optic plates (*OpPl*) and rudiments of antennæ (*AntR*). × 40.

D.—Longitudinal section of one of the antennal rudiments. × 156.

PLATE 3

Larva of the honeybee

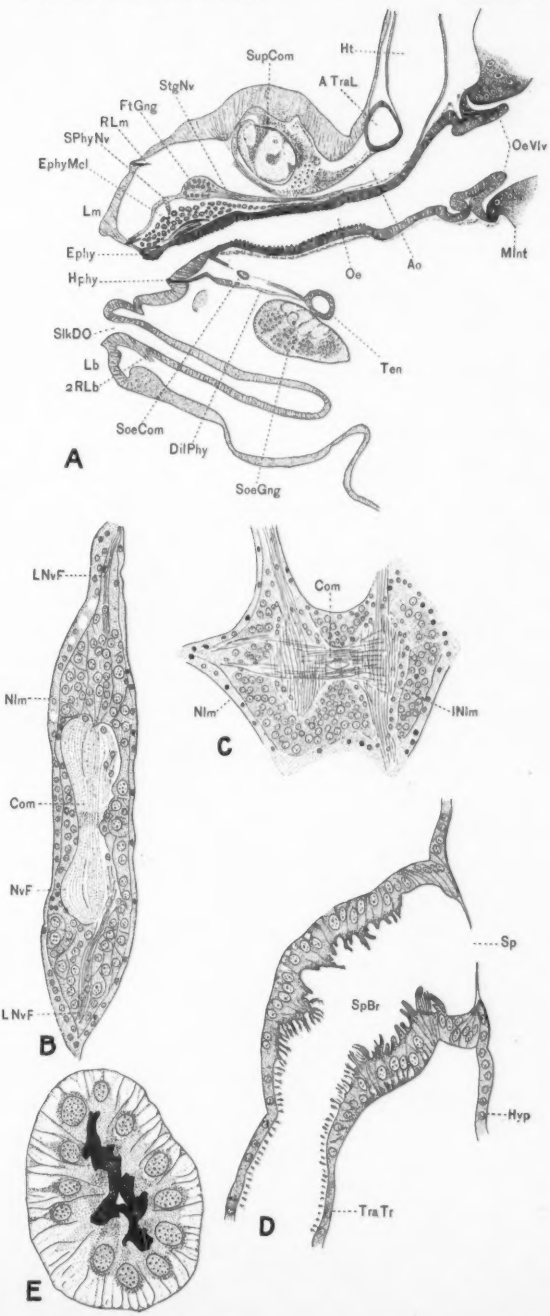
A.—Sagittal section through head of mature larva. × 57.

B.—Cross section of a thoracic ganglion. × 205.

C.—Horizontal (coronal) section of a thoracic ganglion. × 153.

D.—Longitudinal section of a spiracular branch, intersecting spiracle (*Sp*). × 195.

E.—Cross section of a spiracular branch of a mature larva. × 195.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Morphology of the Honeybee Larva

PLATE 4

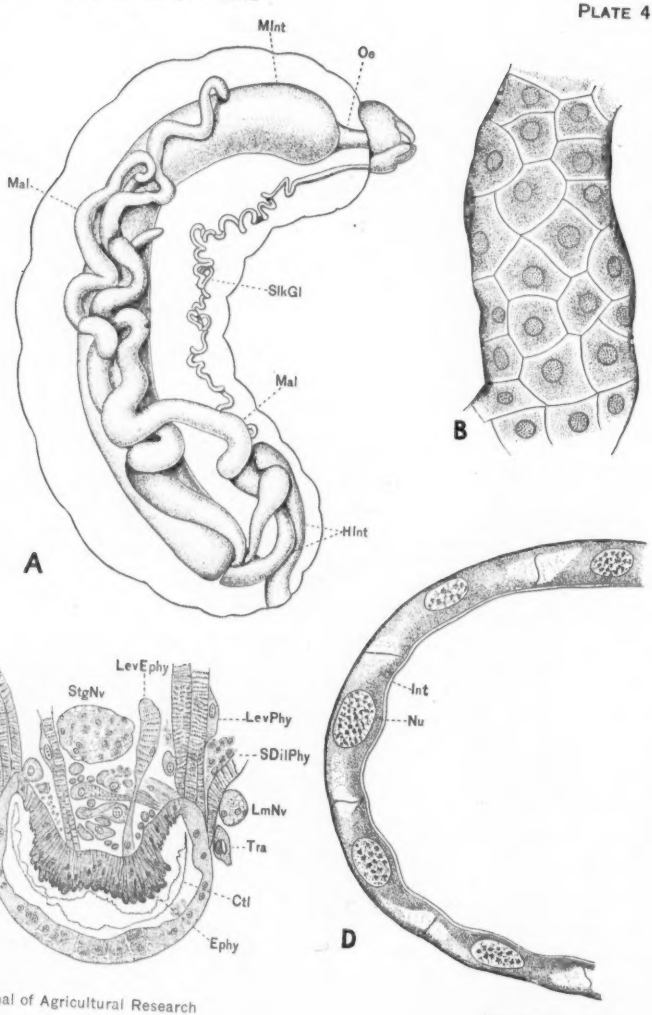


PLATE 4

Larva of the honeybee

A.—Alimentary canal, silk glands (*SlkGl*), and Malpighian tubules (*Mal*) of a mature larva, drawn from a dissection. × 10.

B.—Surface view of a short section of a Malpighian tubule. × 75.

C.—Cross section of pharynx, just caudad of frontal ganglion. × 152.

D.—Cross section of Malpighian tubule. × 300.

PLATE 5

Larva of the honeybee

A.—Cross section through the first abdominal segment of mature larva. × 20.

B.—Section of wall of mid-intestine of old larva, showing imaginal cells (*ImCls*) and striated border (*StrBr*). × 235.

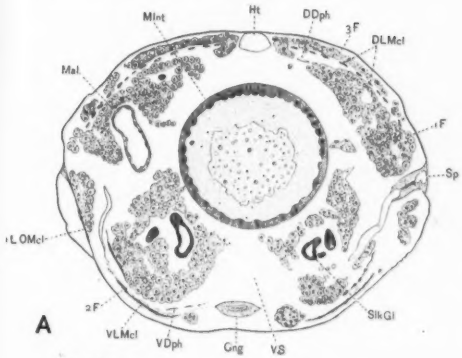
C.—Junction of wall of mid-intestine and oesophagus, longitudinal section, showing one-half of oesophageal valve (*OeVlv*). × 120.

D.—Muscles of mid-intestine, seen from their inner (central) surface. × *ca* 80.

E.—Cross section of hind intestine, showing folds. × 144.

F.—Cross section of silk gland, near the fifth abdominal segment. × 235.

G.—Cross section of silk gland, near its anterior end. × 235.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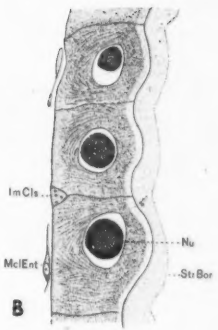
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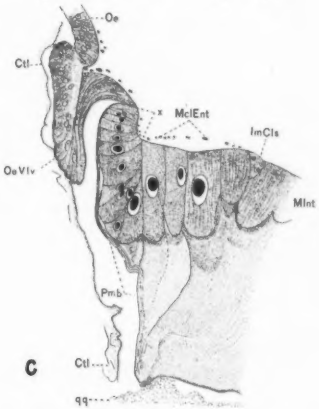
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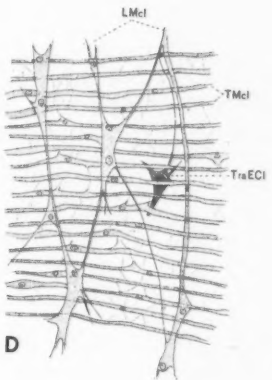
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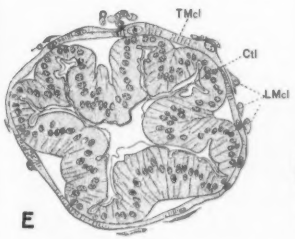
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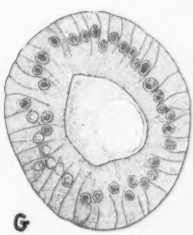
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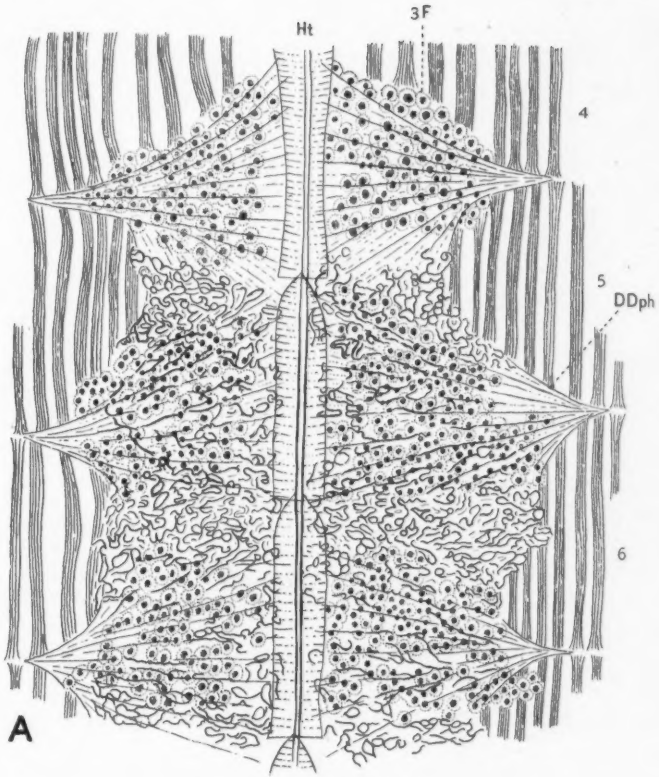
PLATE 7

Larva of the honeybee

A.—Dorsal diaphragm and heart, fourth, fifth, and sixth abdominal segments, viewed from the inner surface. Diaphragm cells represented by heavy wavy lines. × 63.

B.—Transverse section of heart (*Ht*), taken near the anterior end of the abdomen. × 315.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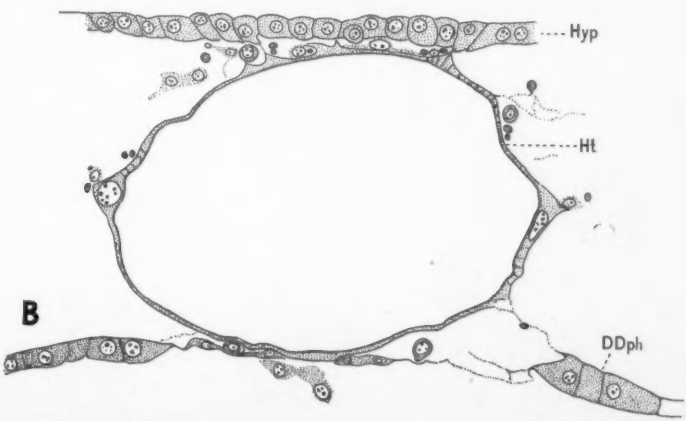
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PLATE 8

Larva of the honeybee

A.—Four fat cells from advanced worker larva, showing fat globules blackened by osmic acid.

B.—Oenocyte (*Oen*) and fat cell (*F*), from a mature larva. × 406.

C.—Urate cells (*u*) and fat cell (*F*), from a mature larva. × 406.

D.—Fat cells (*F*), oenocytes (*Oen*), and urate cells (*u*), from a larva about two days old, showing the crowding of the nuclei toward the side of the cells. × 406.

E.—Four fat cells from a larva 3 days old. × 406.

F.—Three fat cells from a larva 3 to 4 days old. × 406.

G.—Transverse section through heart (*Ht*) and rudiments of ovaries (*Ov*) of a mature worker larva. × 18.

H.—Transverse section through the rudiment of an ovary of a mature worker larva, taken near the posterior end of the rudiment. × 176.

I.—Side view of rudiment of ovary of mature worker larva, showing r udiment of oviduct (*Ovd*). × 28.

J.—Rudiment of testis of drone larva, side view. × 9.

K, L.—Rudiments of ovary of worker larva and queen larva, respectively. × 9.

EFFECT OF WINTER RATIONS ON SUBSEQUENT PASTURE GAINS OF STEERS[1]

By E. W. SHEETS

Assistant Chief, Animal Husbandry Division, Bureau of Animal Industry, United States Department of Agriculture[2]

OBJECT AND PLAN OF THE WORK

To determine the influence of several winter rations on the gains of 2-year-old steers in the following summer on pasture, an experiment was carried on for three years. This experiment is part of a series of experiments on beef-production problems in the Appalachian Mountain region that have been in progress since December 22, 1914, in cooperation between the Bureau of Animal Industry of the United States Department of Agriculture and the West Virginia Agricultural Experiment Station, on the farm of David Tuckwiller, in Greenbrier County, W. Va. This farm is situated in the southeastern part of the State in the blue-grass area.

FIG. 1.—Region to which this work applies. The black dot indicates the location of the farm on which the experiment was conducted. The shaded portion represents the area to which the results are applicable, and the dotted portion shows an additional area to which the results apply in part

The results of similar work with cows, calves, and yearlings are published in United States Department of Agriculture Bulletins 1024, 1042, and 870, respectively.

The work was carried on for three years in order to have an average of feeds, cattle, seasons, and other conditions tending to produce variation. A general outline of the experiment, including the feeds used for the different lots of steers, is given in Table I.

[1] Received for publication May 19, 1924—issued Nov., 1924. This experiment is reported in full in United States Department of Agriculture Bulletin 1251.

[2] Arthur T. Semple and R. H. Tuckwiller, Animal Husbandry Division, United States Department of Agriculture and E. A. Livesay of the West Virginia Agricultural Experiment Station assisted in this study.

TABLE I.—*Outline of the three years' work*

Lot No.	Season	Steers in lot [a]	Winter periods [b]		Summer periods on pasture [c]
			Duration	Feed	
			Days		*Days*
1	1919–20	10	127	Mixed hay and ear corn	136
	1920–21	10	121		128
	1921–22	10	124		141
2	1919–20	9	127	Corn silage	136
	1920–21	10	121		128
	1921–22	10	124		141
3	1919–20	10	127	do	136
	1920–21	10	121		128
	1921–22	10	124		141
4	1919–20	10	127	Corn silage and cottonseed meal	136
	1920–21	10	121		128
	1921–22	10	124		141
5	1919–20	10	127	Corn silage, cottonseed meal, and wheat straw	136
	1920–21	8	121		128
	1921–22	10	124		141
6	1919–20	10	127	Corn silage and mixed hay	136
	1920–21	10	121		128
	1921–22	10	124		141

[a] Owing to accidents 1 steer died in Lot 2 in the summer of 1919–20 and 2 steers died in Lot 5 in the winter of 1920–21; averages for Lot 2 are based on 29 steers and for Lot 5 on 28 steers in subsequent tables.

[b] 1919–20, Dec. 23 to Apr. 27, inclusive; 1920–21, Dec. 28 to Apr. 27, inclusive; 1921–22, Dec. 23 to Apr. 25, inclusive. The average length of period is 124 days.

[c] 1919–20, Apr. 28 to Sept. 10, inclusive; 1920–21, Apr. 28 to Sept. 2, inclusive; 1921–22, Apr. 26 to Sept. 13, inclusive. The average length of period is 135 days.

KINDS OF STEERS USED

The steers used were long 2-year-old grade Shorthorn, Hereford, and Aberdeen Angus, raised in southern West Virginia. They were good feeder steers, quite uniform in quality and condition. They ranged in weight from 800 to 1,200 pounds and averaged 964 pounds at the beginning of the winter periods.

METHOD OF FEEDING AND HANDLING THE STEERS

In the fall before starting the steers on winter feed they were divided into lots of 10 each. In making this division, care was taken to have the lots as nearly uniform as possible in quality, breeding, size, and condition. The different lots were given the same amount of space in an open barn and were kept under cover all winter. Water was supplied in the stalls at all times and salt was constantly available. The steers were fed twice a day.

The feed, both concentrates and roughage, was carefully weighed at each feeding. All the feeds used were of good quality. There was practically no waste. The steers were weighed for three consecutive days at the beginning and at the end of the winter period. They were also weighed once every 28 days. All weighings were made in the morning after feeding. Neck straps and disks or ear tags with numbers on them were used, so that ready identification of each individual could be made and records accurately kept.

In the spring of each year, as soon as the grass was good enough, which was usually about April 25, the steers from all the lots were turned into a rather hilly pasture of about 300 acres with no additional feed. A good growth of blue grass with white clover is found on all parts of the pasture. A small stream, which flows through the pasture, provides an abundance of fresh water throughout the summer. The soil is of limestone formation. Under normal climatic conditions there is sufficient rainfall to keep the grass growing throughout the season

Weights were taken once every 28 days during the first summer. Afterwards the practice was discontinued on account of the loss incident to driving such heavy steers the long distance from the pastures to the scales. During the second summer they were weighed only on the sixty-second day and during the third summer only on the forty-fourth day. Three consecutive daily weights were not taken at the end of the grazing season, on account of the incident loss in weight. Each year the steers were marketed in Jersey City at the end of the summer grazing period.

QUANTITY OF FEED CONSUMED

Table II shows the total quantities of different feeds eaten by the various lots and the average daily ration per steer in each lot during each of the three winters. All lots except Lot No. 2 were fed to make a small gain in weight. Lot No. 1 failed to gain in weight in the winter of 1921–22 on account of the poor quality of the mixed hay. They would not eat enough of it to maintain their weight. It was planned to feed Lot No. 2 so that it would lose slightly in weight. This object was not attained the first year. The quantities of feed consumed daily were practically the same throughout the winter periods. Lot No. 3 was given practically as much silage as the steers would clean up.

TABLE II.—*Average total and daily rations per steer during winters*

Winter feed	Total feed per steer			Average	Daily feed per steer			Average
	1919–20	1920–21	1921–22		1919–20	1920–21	1921–22	
Lot 1:	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*
Mixed hay	2,540	2,403	1,860	2,268	20.0	19.9	15.0	18.3
Ear corn	254	242	245	247	2.0	2.0	2.0	2.0
Lot 2: Corn silage	3,810	3,490	3,487	3,588	30.0	28.8	28.1	28.9
Lot 3: Corn silage	5,080	4,840	4,478	4,799	40.0	40.0	36.1	38.7
Lot 4:								
Corn silage	3,810	3,490	3,683	3,661	30.0	28.8	29.7	29.5
Cottonseed meal	190	181	184	185	1.5	1.5	1.5	1.5
Lot 5:								
Corn silage	3,125	3,025	3,069	3,076	25.0	25.0	24.7	24.8
Wheat straw	734	698	736	725	5.8	5.8	5.9	5.8
Cottonseed meal	127	121	123	124	1.0	1.0	1.0	1.0
Lot 6:								
Corn silage	3,125	3,025	3,069	3,073	25.0	25.0	24.7	24.8
Mixed hay	1,016	968	749	911	8.0	8.0	6.0	7.3

As Table III shows, there was considerable variation in the nutritive ratio of the rations as fed as well as in the quantities of dry matter and digestible nutrients in them. The rations containing hay and straw were especially high in dry matter. The rations of silage alone were lowest in digestible protein, while that containing 1.5 pounds of cottonseed meal was considerably the highest. The rations containing cottonseed meal had nutritive ratios considerably narrower than the others.

TABLE III.—*Quantities of dry matter, digestible nutrients, and nutritive ratios of the rations*

Lot No.	Winter ration per steer	Digestible nutrients			Nutritive ratio	Feed per 1,000 pounds live weight [b]
		Dry matter	Protein	Carbohydrate equivalent [a]		
		Pounds	*Pounds*	*Pounds*		
1	Mixed hay (18.3 pounds)	17.0	0.63	9.08		19.0
	Ear corn (2.0 pounds)	1.8	0.07	1.38		2.1
	Total	18.8	0.70	10.46	1 : 14.9	
2	Corn silage (28.9 pounds)	7.8	0.37	4.99	1 : 13.5	30.1
3	Corn silage (38.7 pounds)	10.5	0.49	6.67	1 : 13.5	40.1
4	Corn silage (29.5 pounds)	8.0	0.38	5.09		30.6
	Cottonseed meal (1.5 pounds)	1.4	0.53	0.61		1.6
	Total	9.4	0.91	5.70	1 : 6.3	
5	Corn silage (24.8 pounds)	6.7	0.32	4.28		25.7
	Wheat straw (5.8 pounds)	5.4	0.02	2.26		6.0
	Cottonseed meal (1.0 pound)	0.9	0.35	0.41		1.0
	Total	13.0	0.69	6.95	1 : 10.1	
6	Corn silage (24.8 pounds)	6.7	0.32	4.28		25.7
	Mixed hay (7.3 pounds)	6.8	0.25	3.62		7.6
	Total	13.5	0.57	7.90	1 : 13.9	

[a] The carbohydrate equivalent is the sum of the digestible carbohydrates plus 2.25 times the digestible fat.
[b] This is based on the initial weights of the steers.

GAINS DURING WINTER AND SUMMER

The initial spring and final weights and the gains and losses in weight during each of the three years are shown in Table IV.

TABLE IV.—*Average total [a] and daily gains during winter and summer*

Lot No.	Winter feed	Season	Initial weight per steer	Weight per steer at end of winter	Winter gain or loss per steer		Weight per steer at end of summer	Summer gain per steer		Winter and summer gain per steer	
					Total	Daily		Total	Daily	Total	Daily
			Lbs.	*Lbs.*	*Lbs.*	*Lbs.*	*Lbs.*	*Lbs.*	*Lbs.*	*Lbs.*	*Lbs.*
1	Mixed hay and ear corn	1919–20	927	962	35	0.28	1,269	307	2.26	342	1.30
		1920–21	981	1,036	55	0.45	1,321	285	2.23	340	1.37
		1921–22	980	943	−37	−0.30	1,287	344	2.44	307	1.16
	Average		962	980	18	0.14	1,292	312	2.31	330	1.27
2	Corn silage	1919–20	913	950	37	0.29	1,236	286	2.10	323	1.23
		1920–21	961	927	−54	−0.45	1,290	363	2.84	309	1.24
		1921–22	983	977	−6	−0.05	1,361	384	2.72	378	1.43
	Average		961	952	−9	−0.07	1,298	346	2.56	337	1.30
3	Corn silage	1919–20	928	1,007	79	0.62	1,246	239	1.76	318	1.21
		1920–21	987	1,033	46	0.38	1,338	305	2.38	351	1.41
		1921–22	981	1,053	72	0.58	1,359	306	2.17	378	1.43
	Average		965	1,031	66	0.53	1,314	283	2.10	349	1.35
4	Corn silage and cottonseed meal.	1919–20	927	994	67	0.53	1,291	297	2.18	364	1.38
		1920–21	983	998	15	0.12	1,314	316	2.47	331	1.33
		1921–22	982	1,051	69	0.56	1,373	322	2.28	391	1.48
	Average		964	1,014	50	0.40	1,326	312	2.31	362	1.40
5	Corn silage, wheat straw, and cottonseed meal.	1919–20	927	1,020	93	0.73	1,270	250	1.84	343	1.30
		1920–21	987	1,049	62	0.51	1,294	245	1.91	307	1.23
		1921–22	988	1,085	97	0.78	1,365	280	1.99	377	1.42
	Average		966	1,052	86	0.69	1,310	258	1.91	344	1.33
6	Corn silage and mixed hay	1919–20	928	991	63	0.50	1,264	273	2.01	336	1.28
		1920–21	984	1,052	68	0.56	1,295	243	1.90	311	1.25
		1921–22	982	1,028	46	0.37	1,344	316	2.24	362	1.37
	Average		965	1,024	59	0.48	1,301	277	2.05	336	1.30

[a] On account of dropping fractions in the average weights of the steers as given in this table, one can not always add the weights or gains for the 3 years, divide by 3, and obtain the average given. In no case is there more than 1 pound of difference

DIAGRAMS OF GAINS AND LOSSES

The seven charts, Figures 2, 3, 4, 5, 6, 7, and 8 show the gains and losses of the steers by 28-day periods, except as noted under "Method of feeding and handling the steers." The first six show the effect of the six rations under comparison for the three years they were used, one chart being used for each ration. The seventh chart shows the average gains for three years for each of the six rations.

Horizontal distance on the charts indicates the number of days that the steers were fed during the three winters and pastured during the three summers. The average data on which each monthly period began are given also. The average length of the total period for the three years was 259 days, of which 124 days were in the winter period, and the remaining 135 in the summer period.

Vertical distance on the chart represents changes in the live weights of the steers. The weights corresponding to each of the horizontal lines are given along the left side of the chart. As the average initial weight of each lot varied from year to year, the average initial weight per steer for three years is used as a basis in each chart for showing the gains made by each lot each year.

Much of the difference caused by the winter feeding was overcome during the summer. On April 28 there was a difference of 95 pounds between the highest and lowest lots; on June 23, 50 pounds; and on September 10, 33 pounds.

CORRELATIONS

On account of the variations in the average gains of the six lots during the three years, as shown in Table IV, the correlations between the winter, summer, midsummer, and total gains of all the steers based on the losses and gains of each steer have been calculated to substantiate the conclusions indicated by the average gains of each lot for three years. Consequently Figures 9, 10, 11 and 12, are presented to show the positions of the individual steers, when they are plotted according to their winter, summer, midsummer, and total variations in weight. Accordingly, the following results have been obtained:

	Winter gain	Summer gain	Total gain
	Pounds	*Pounds*	*Pounds*
Mean	44.0	297.7	[a] 342.2
Standard deviation	60.1	62.7	57.6

[a] The sum of the mean winter and summer gain is 341.7 while the mean for the total gain is 342.2, the discrepancy being due in all probability to the grouping of the gains in classes of 10 pounds range.

CORRELATIONS

Winter–summer	−0.572	±0.034
Winter–midsummer	− .480	± .038
Winter–total	+ .429	± .041
Summer–total	+ .493	± .038

REGRESSIONS

Total/winter	+0.407
Summer/winter	− .593
Midsummer total/winter	+ .616
Midsummer/winter	− .384

According to the regressions, 100 pounds advantage in weight at the end of the winter is reduced to 61.6 pounds after 54 days on grass and to 40.7 pounds after 136 days on grass. In other words, during the first 54 days on grass, 38.4 pounds is lost of 100 pounds advantage as compared with 21.3 pounds lost during the rest of the summer period of 82 days, making a total loss of 59.3 pounds for the whole summer period.

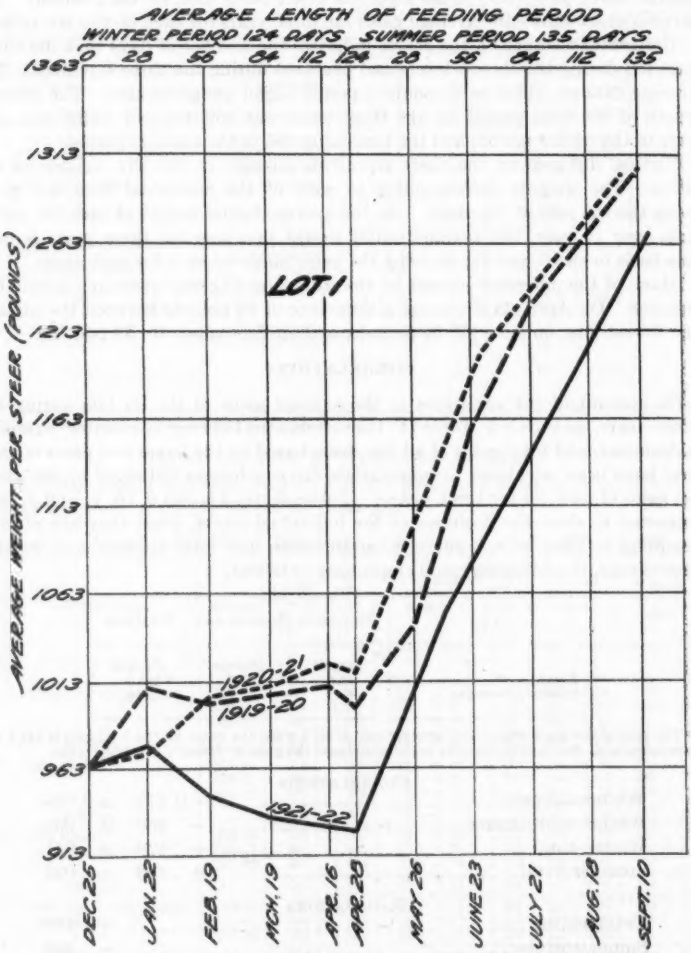


FIG. 2.—Results of winter and summer (grass) feeding for Lot 1. These steers were fed the following average ration during the winter: Mixed hay, 18.3 pounds; ear corn, 2 pounds

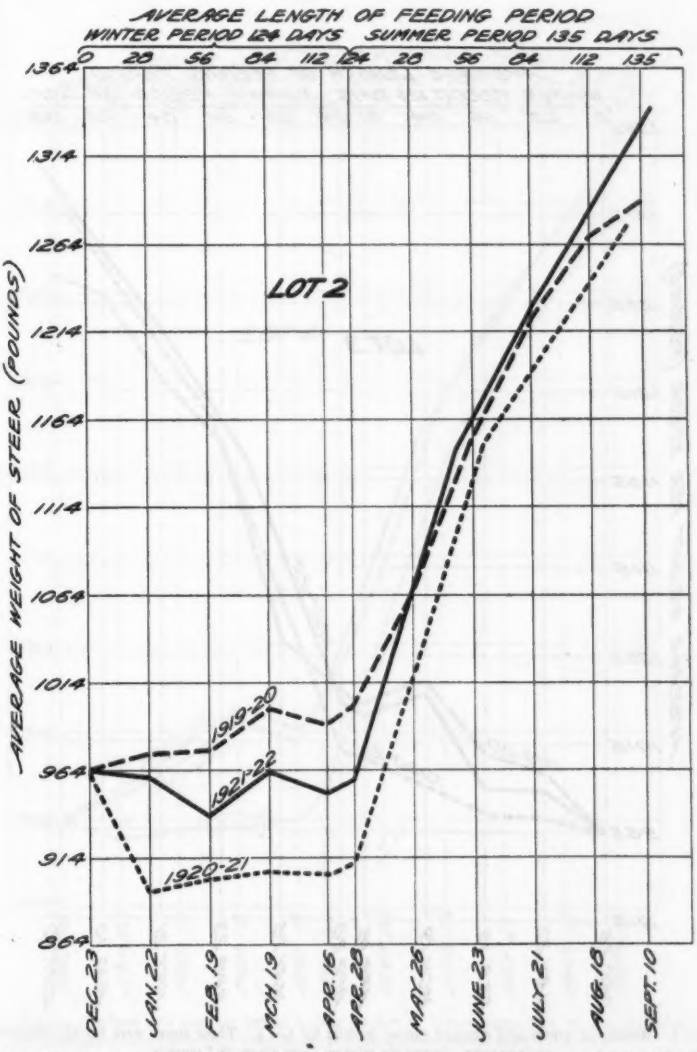


FIG. 3.—Results of winter and summer (grass) feeding for Lot 2. These steers were fed the following average ration during the winter: Corn silage, 28.9 pounds

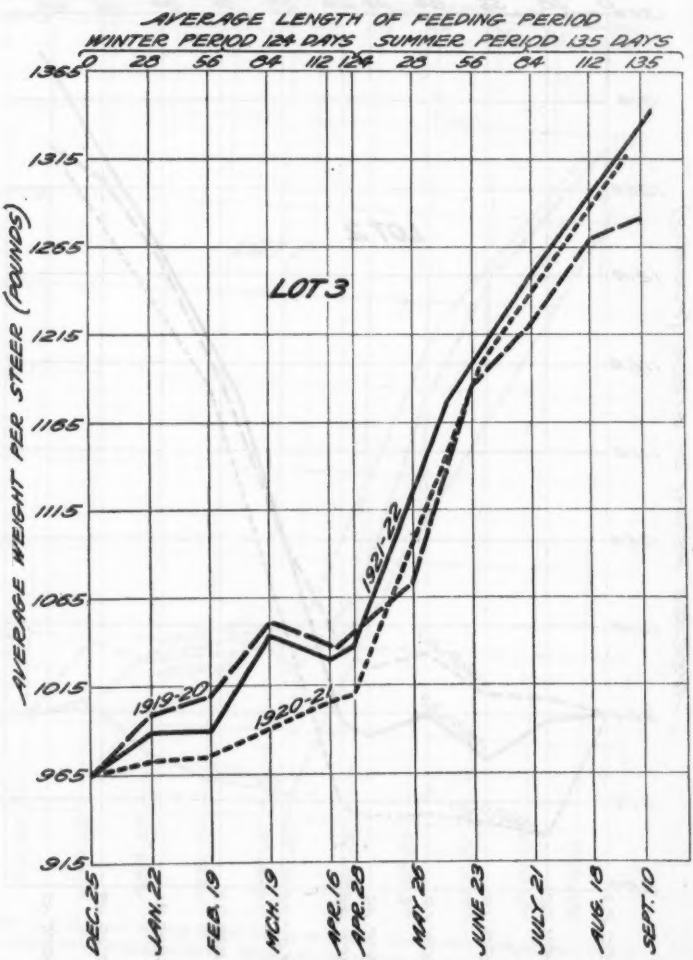


FIG. 4.—Results of winter and summer (grass) feeding for Lot 3. These steers were fed the following average ration during the winter: Corn silage, 38.7 pounds

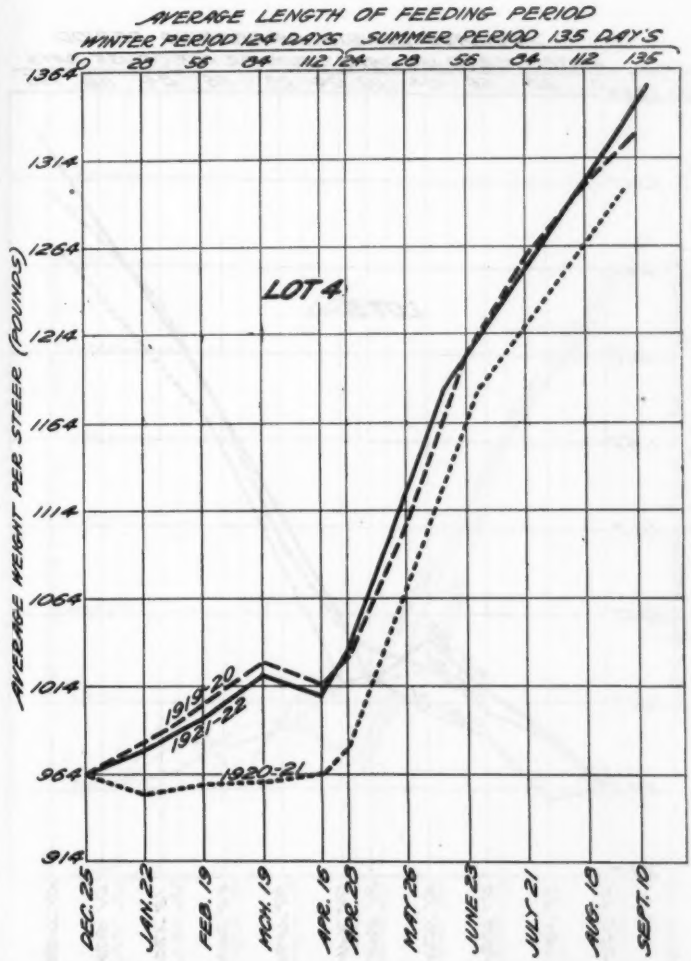


FIG. 5.—Results of winter and summer (grass) feeding for Lot 4. These steers were fed the following averageration during the winter: Corn silage, 29.5 pounds; cottonseed meal, 1.5 pounds

96463—24†——5

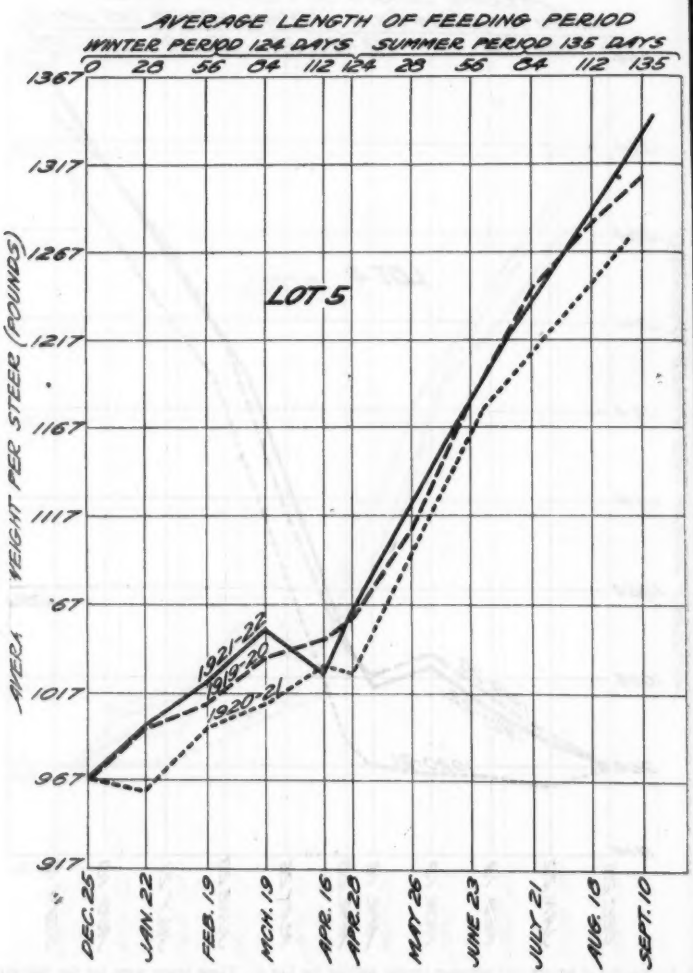


FIG. 6.—Results of winter and summer (grass) feeding for Lot 5. These steers were fed the following average ration during the winter: Corn silage, 24.8 pounds; wheat straw, 5.8 pounds; cottonseed meal 1 pound

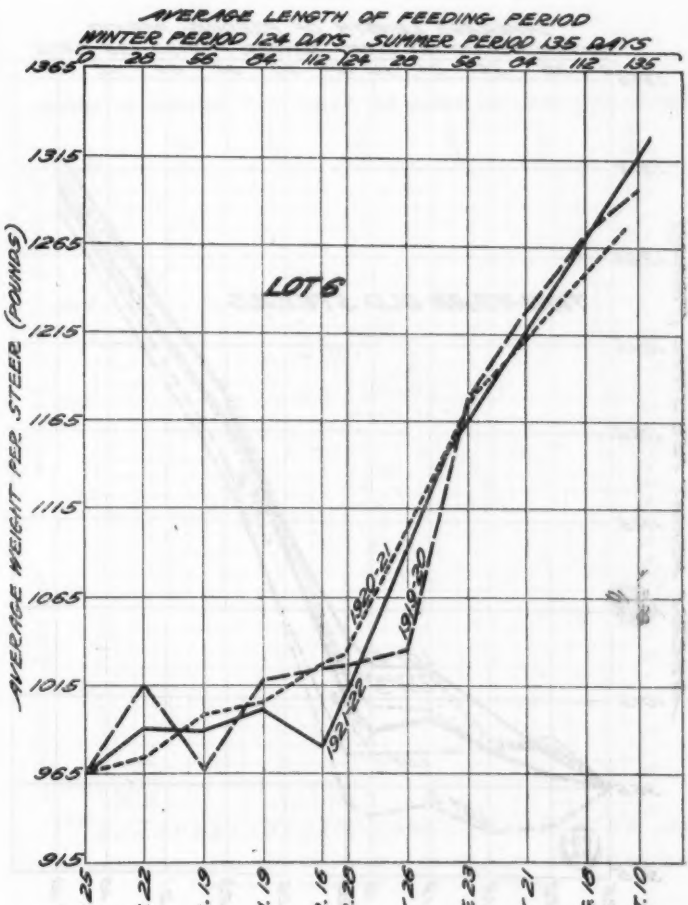


FIG. 7.—Results of winter and summer (grass) feeding for Lot 6. These steers were fed the following average ration during the winter: Corn silage, 24.8 pounds; mixed hay, 7.3 pounds

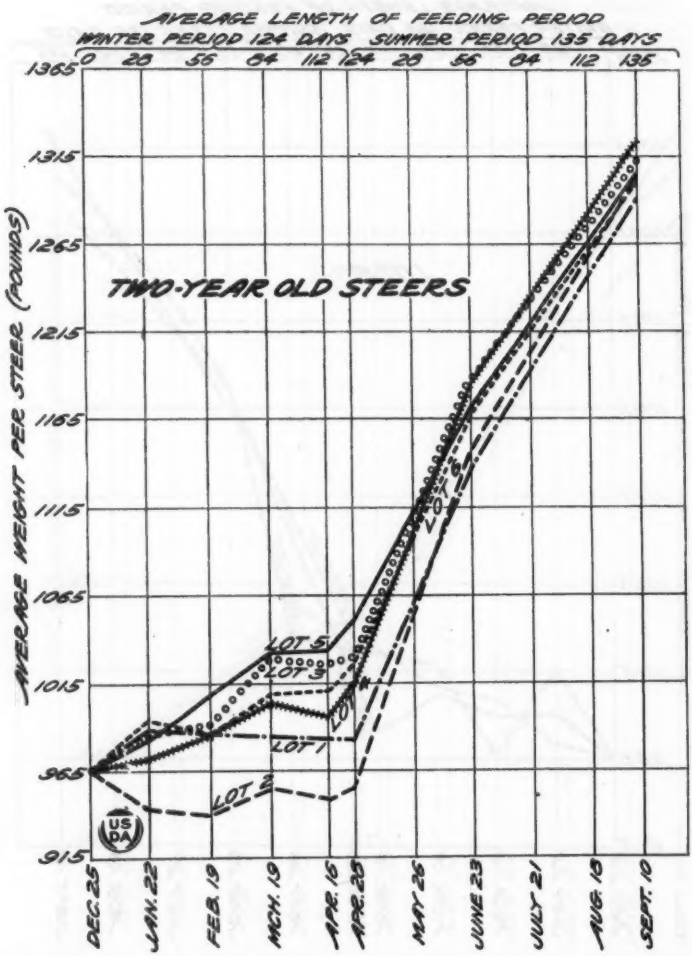


FIG. 8.—Average results of three years' winter and summer (grass) feeding for the six lots of steers

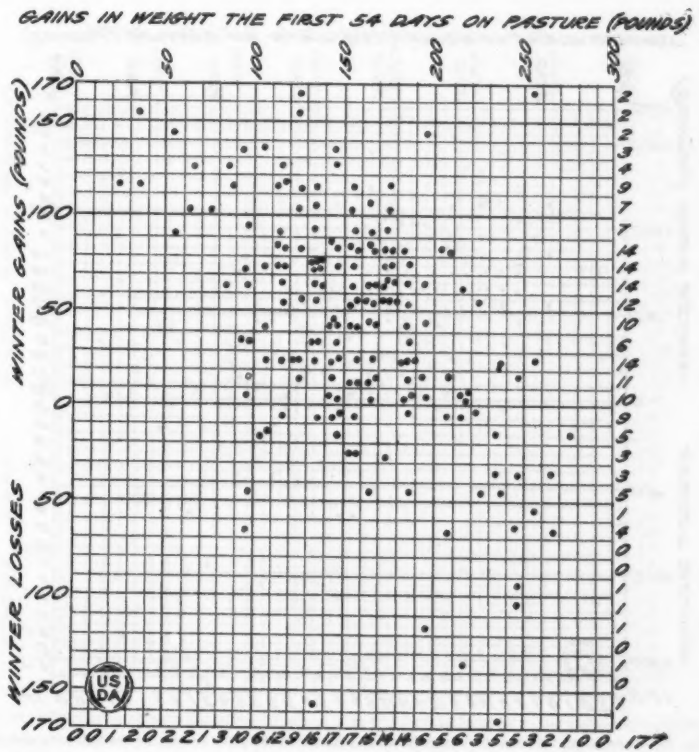


FIG. 9.—Correlation between the winter losses and gains and the gains for the first 54 days (average for three years) on pasture, based on the individual steers

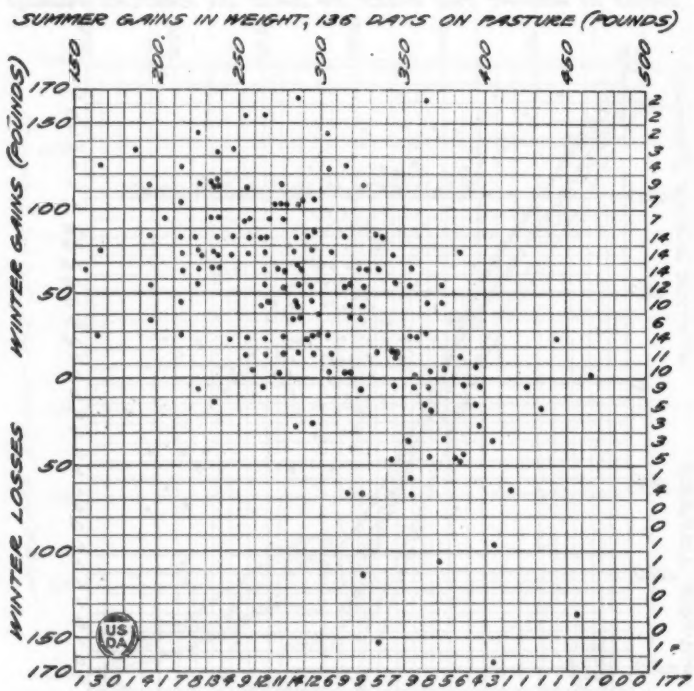


FIG. 10.—Correlation between the winter losses and gains and the gains on pasture the following summer based on the individual steers

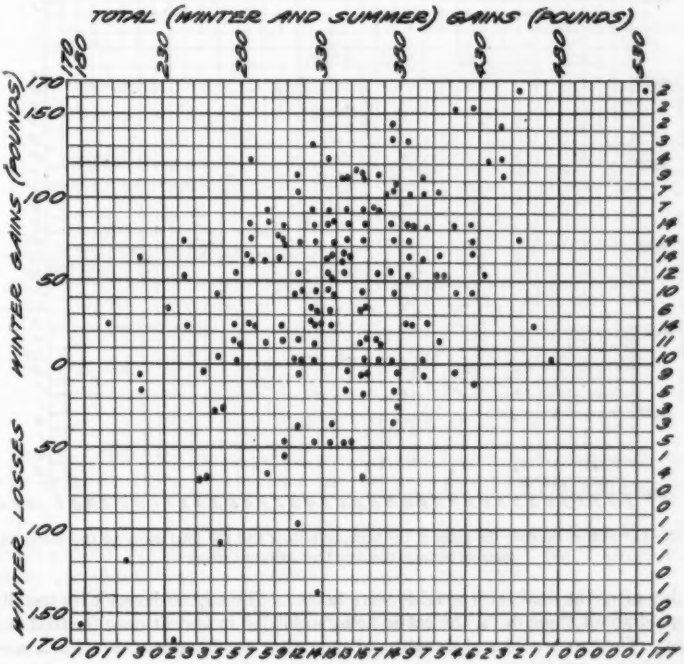


FIG. 11.—Correlation between the winter losses and gains and the total gains for winter and summer periods, based on the individual steers

SHRINKAGE IN TRANSIT AND DRESSING PERCENTAGE

The shrinkage in transit, commonly called "drift" in the Appalachian region, and the dressing percentages are given in Table V for the first two years. Owing to conditions incident to marketing the cattle, the data at the end of the third summer were not obtained. They were shipped either on the same day or on

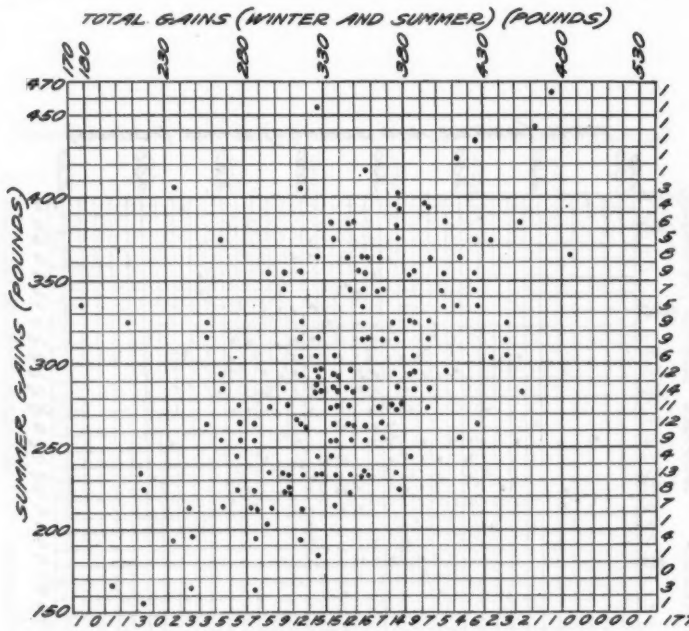


FIG. 12.—Correlation between the gains of the summer periods and the total gains for the winter and summer periods, based on the individual steers

the day after the final farm weights were taken. The trip to Jersey City usually occupied about three days, the cattle being unloaded in transit once for feed and water. They were sold and slaughtered soon after reaching market. Variations in shrinkage and dressing percentage of the several lots are not considered to be sufficiently large for drawing conclusions relative to the methods of winter feeding. However, it should be noted that Lot No. 4, which made the largest gain for the year, dressed highest, and that Lot No. 1, which made the least gain, dressed lowest.

TABLE V.—*Market weight, shrinkage in transit, and dressing percentage per steer for the first and second years' work*

Lot No	Winter feed	Season	Market weight	Shrinkage, or "drift," in transit	Percentage of drift	Dressed weight	Farm weight dressing percentage	Market weight dressing percentage
			Pounds	*Pounds*	*Per cent*	*Pounds*	*Per cent*	*Per cent*
1	Mixed hay and ear corn	1919–20	1,203	66	5.2	673	53.0	55.9
		1920–21	1,244	77	5.8	687	52.0	55.2
	Average		1,223	71	5.5	680	52.5	55.6
2	Corn silage	1919–20	1,174	62	5.0	668	54.0	56.9
		1920–21	1,202	88	6.8	685	53.1	57.0
	Average		1,189	75	5.9	676	53.5	56.9
3	Corn silage	1919–20	1,187	50	4.7	677	54.3	57.0
		1920–21	1,246	92	6.9	709	53.0	56.9
	Average		1,216	75	5.8	693	53.6	57.0
4	Corn silage and cottonseed meal	1919–20	1,225	66	5.1	704	54.5	57.4
		1920–21	1,229	85	6.5	699	53.2	56.9
	Average		1,227	75	5.8	701	53.8	57.1
5	Corn silage, wheat straw, and cottonseed meal.	1919–20	1,223	47	3.7	681	53.6	55.7
		1920–21	1,215	79	6.1	694	53.6	57.1
	Average		1,220	61	4.8	687	53.6	56.3
6	Corn silage and mixed hay	1919–20	1,187	77	6.1	679	53.7	57.2
		1920–21	1,211	84	6.5	684	52.8	56.5
	Average		1,199	80	6.3	681	53.2	56.8

CONCLUSIONS

On the whole, the steers which made larger winter gains also made larger total gains for the year when fattened on grass the following summer (correlation, 0.43).

The steers which made only slight gains or lost weight during the winter made greater summer gains on pasture than steers which made larger winter gains (correlation between winter and summer gains, −0.57).

Consequently, differences in weight of steers at the end of the winter, due to rations fed, are gradually minimized during the time of summer fattening on grass. An advantage of 100 pounds at the end of winter falls to one of only 41 pounds after 136 days on grass.

Since differences in weight due to winter feeding are gradually minimized, but not wholly overcome, during the summer season of fattening on grass, it is important that cattle to be marketed early should gain considerably more weight during the winter than if they are to be marketed late. An advantage of 100 pounds at the end of winter falls to one of 62 pounds after 54 days on grass.

There is so little difference between the gains made by the steers in the different lots at the end of the summer grazing period that any conclusion as to the best winter ration must take into consideration the cost of the ration.

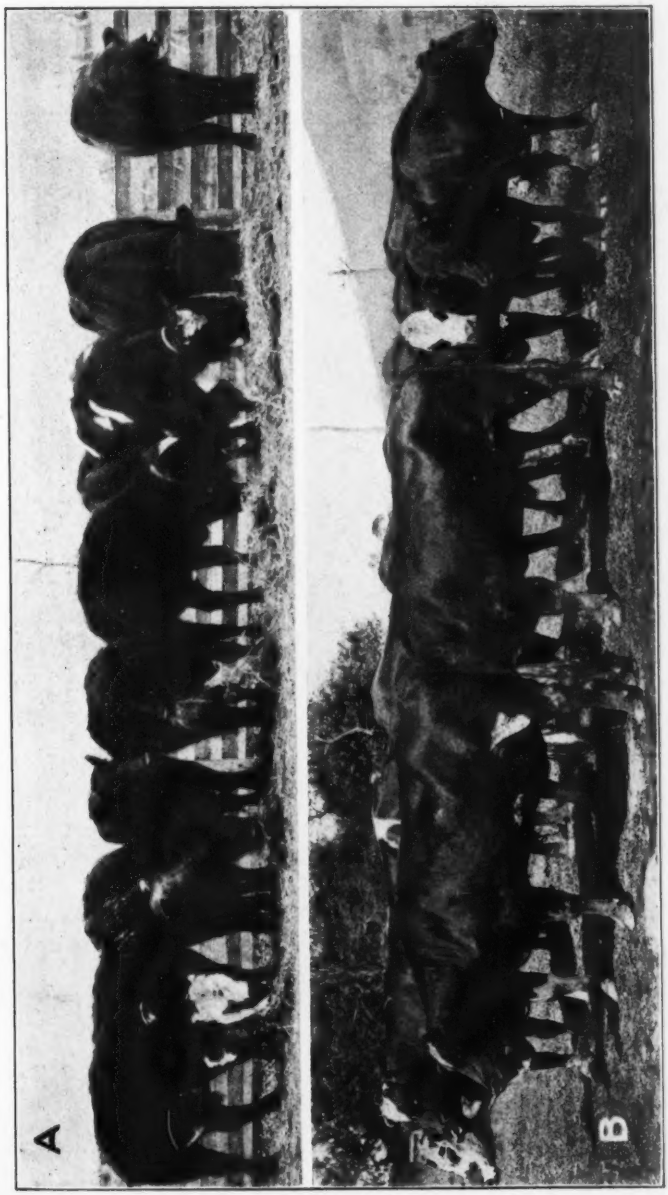
Succulent rations of silage alone, or silage, cottonseed meal, and straw, or silage and mixed hay, as used in this experiment, are cheaper and produce greater gains for the year than a dry ration of mixed hay and ear corn.

96463—24†——6

PLATE 1

A.—Lot 1 at the beginning of the third year's work; winter ration, mixed hay, 15 pounds; ear corn, 2 pounds.

B.—Lot 1 at the end of the third year's work; average gain per steer, 307 pounds.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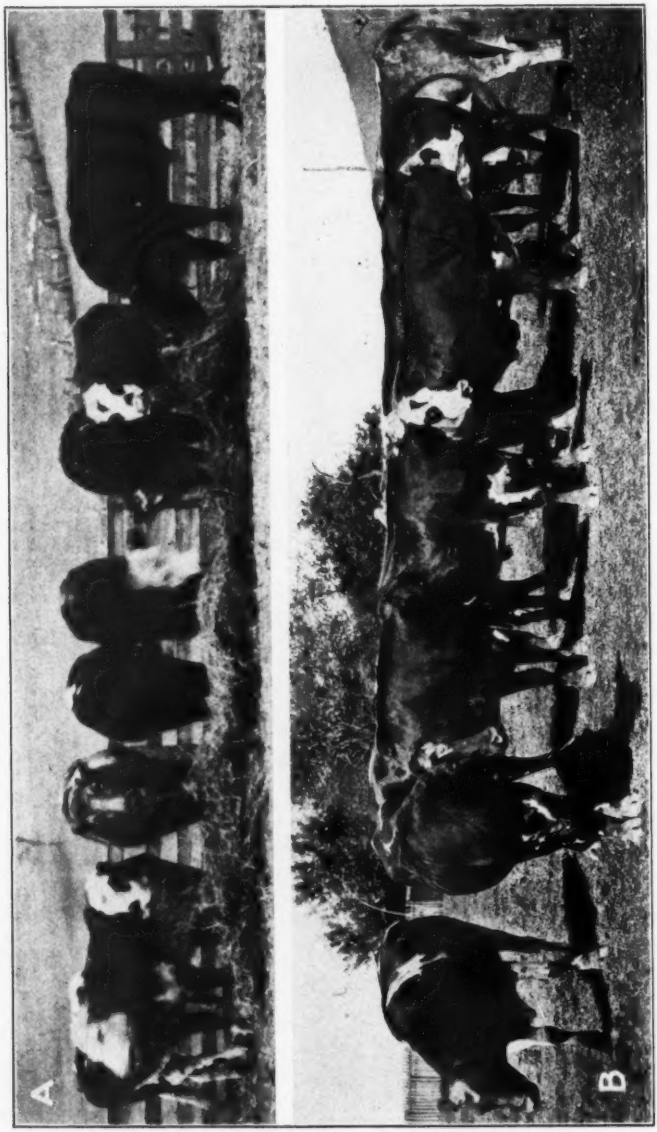
A
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PLATE 2

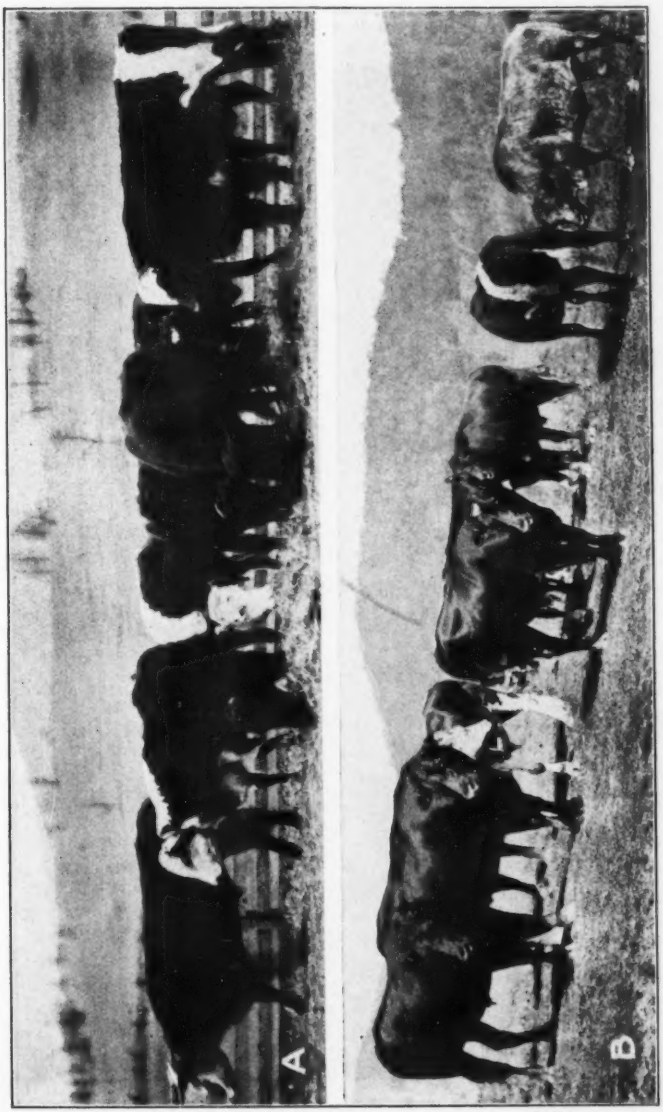
A.—Lot 2 at the beginning of the third year's work; winter ration, silage, 28 pounds.

B.—Lot 2 at the end of the third year's work; average gain per steer, 378 pounds.

PLATE 3

A.—Lot 3 at the beginning of the third year's work; winter ration, silage, 36 pounds.

B.—Lot 3 at the end of the third year's work; average gain per steer, 378 pounds.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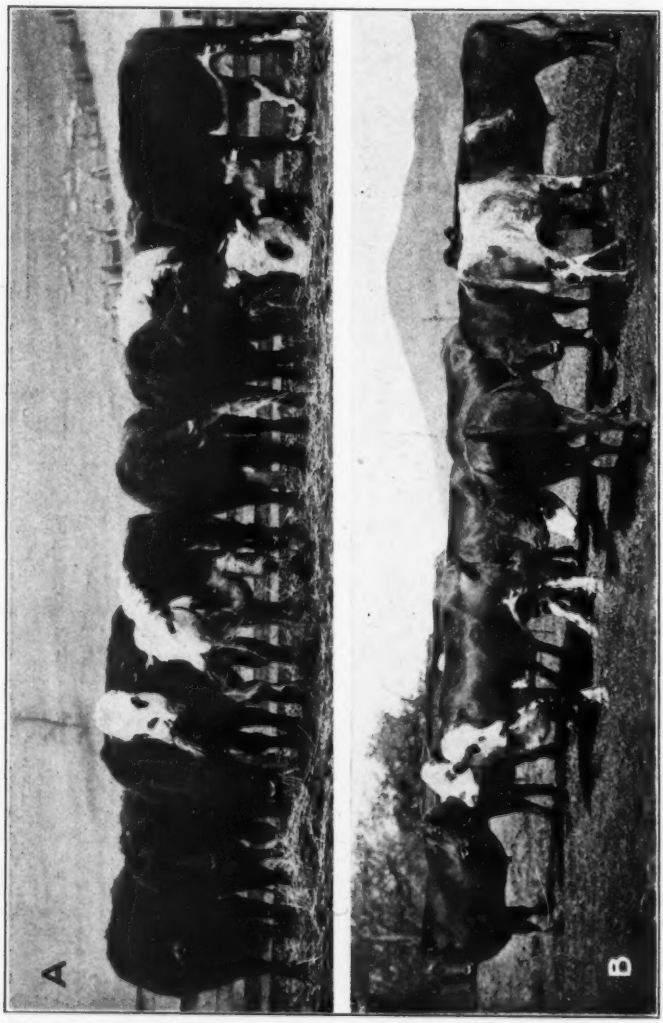

A
B

PLATE 4

A.—Lot 4 at the beginning of the third year's work; winter ration, silage 30 pounds; cottonseed meal, 1.5 pounds.

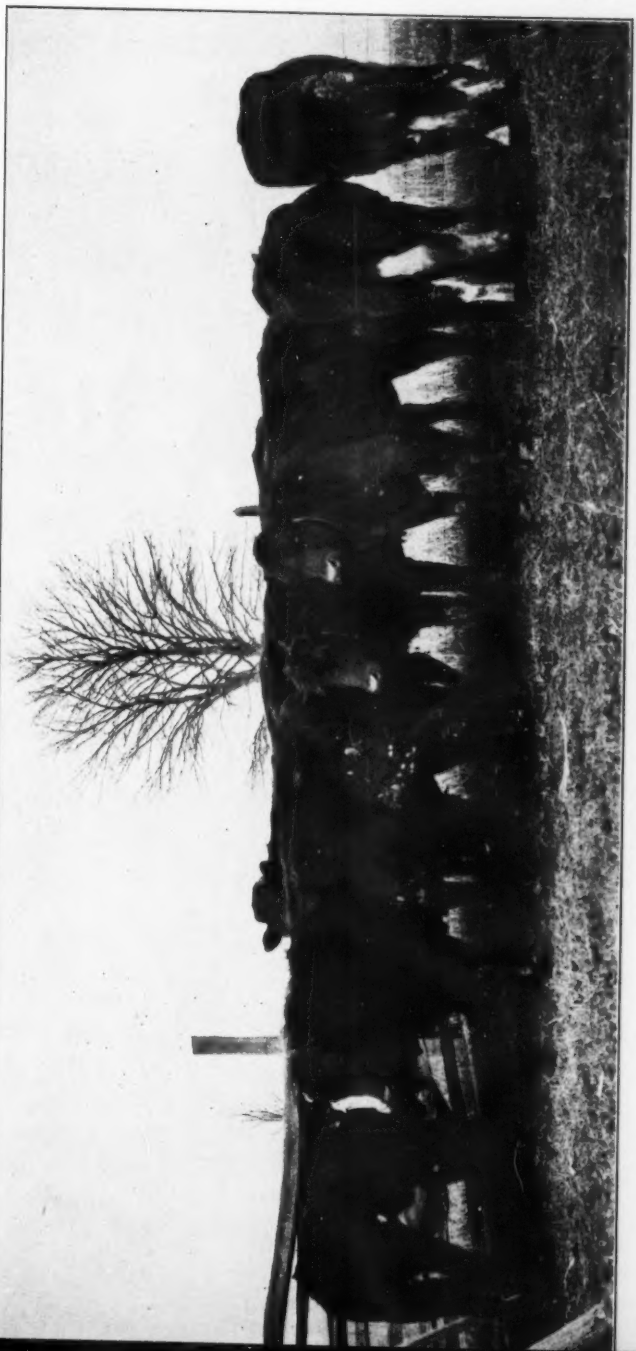
B.—Lot 4 at the end of the third year's work; average gain per steer, 391 pounds.

PLATE 5

Lot 5 at the end of the first winter feeding period, April 22, 1920. They represent the type of steers used in the first year's work. Aberdeen Angus breeding predominated.

Effect of Winter Rations on Pasture Gains of Steers

PLATE 6



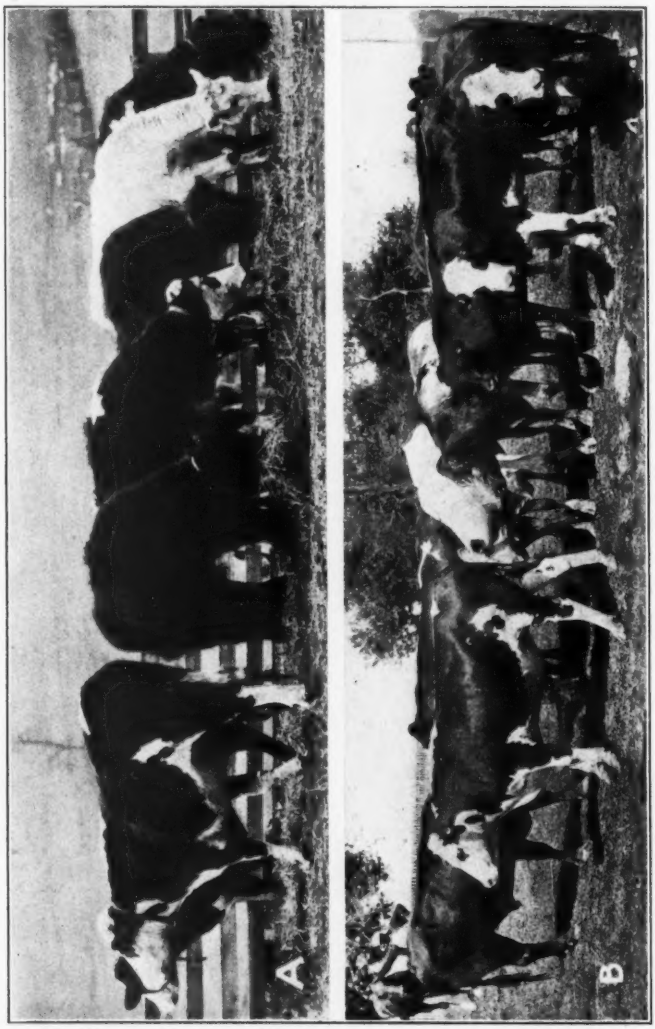

A
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PLATE 6

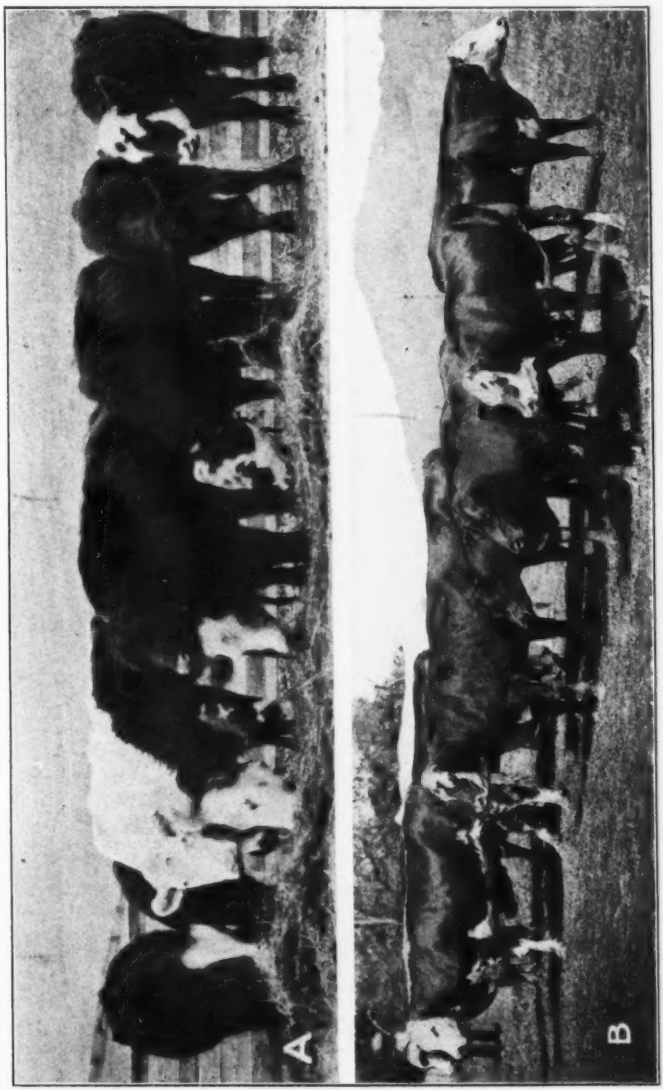
A.—Lot 5 at the beginning of the third year's work; winter rations, silage, 25 pounds; straw, 6 pounds; cottonseed meal, 1 pound.

B.—Lot 5 at the end of the third year's work; average gain per steer, 377 pounds.

PLATE 7

A.—Lot 6 at the beginning of the third year's work; winter ration, silage 25 pounds; mixed hay, 6 pounds.

B.—Lot 6 at the end of the third year's work; average gain per steer, 362 pounds.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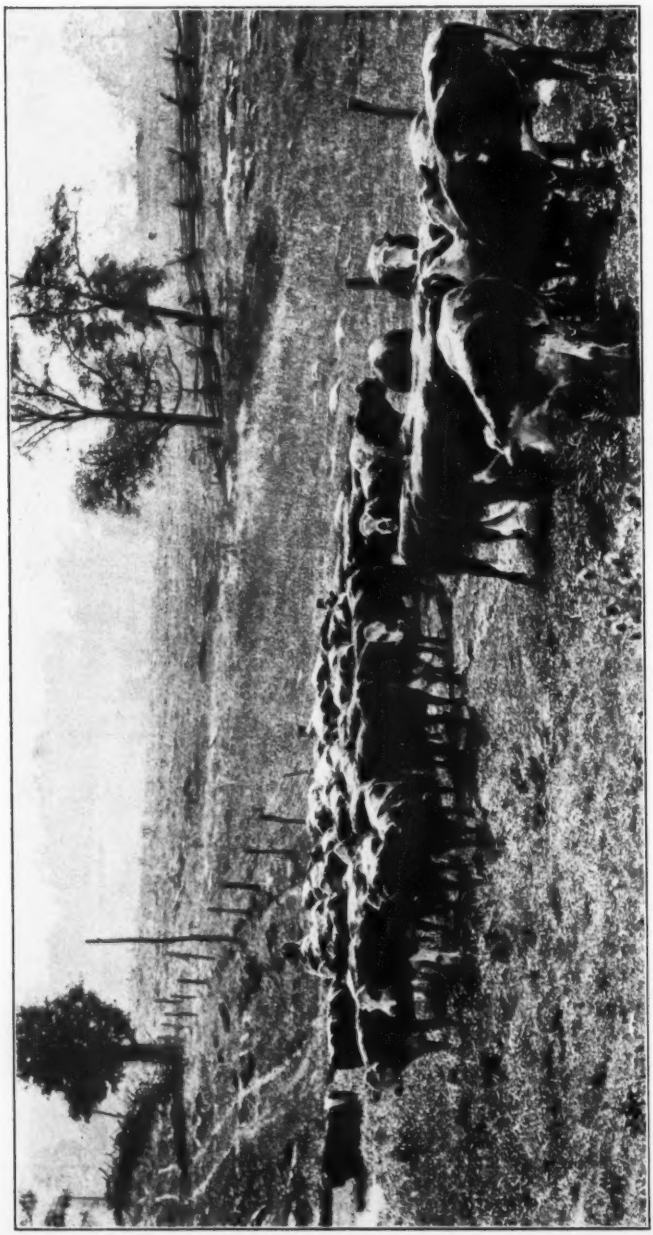
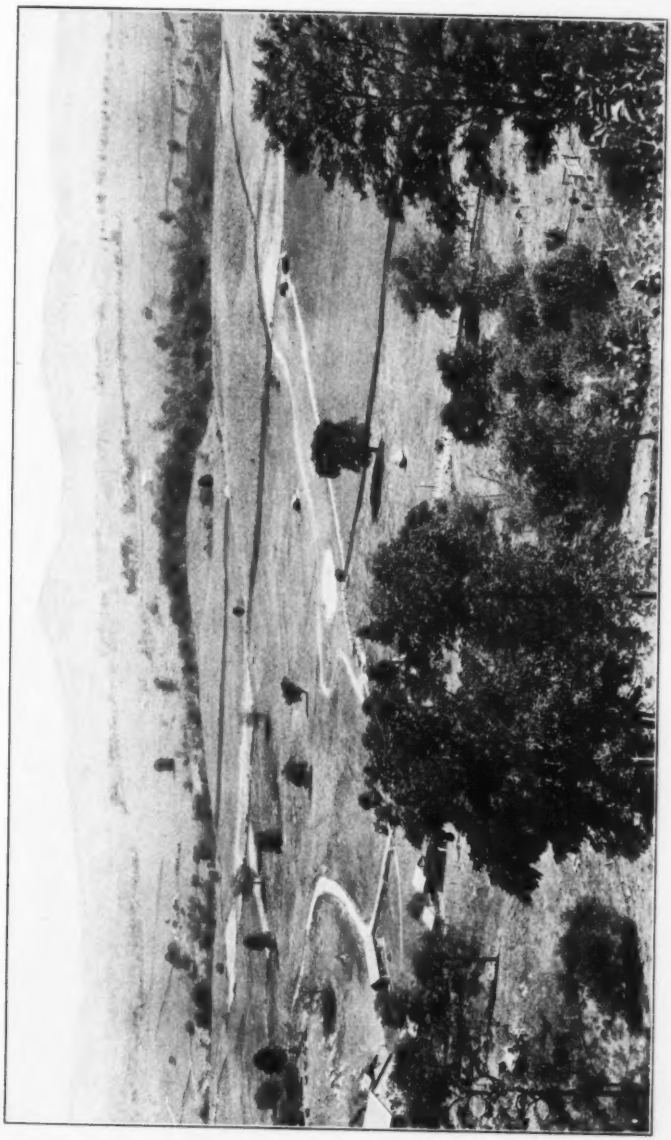


PLATE 8

The six lots of steers in September, 1922, at the lower corner of their pasture. They are about to be driven 5 miles to be loaded and shipped to Jersey City.

PLATE 9

Looking from Muddy Creek Mountain across a branch of the Greenbrier Valley. The steers were fattened on a pasture at the foot of the mountains in the upper part of the picture.



A STUDY OF DOUGLAS FIR REPRODUCTION UNDER VARIOUS CUTTING METHODS [1]

By JACOB ROESER, Jr., *Forest Examiner, Fremont Forest Experiment Station, Forest Service, United States Department of Agriculture*

In the fall of 1913, four plots, each 200 by 200 feet, and subdivided into 20-foot sections, were laid out in a typical Douglas fir (*Pseudotsuga taxifolia*) stand in the vicinity of the Fremont Forest Experiment Station, on a north exposure, with a fairly uniform slope of approximately 35 per cent and an elevation of 9,100 feet. The merchantable stand was approximately 265 years old and consisted of Douglas fir and Engelmann spruce (*Picea engelmanni*) in mixture with some limber pine (*Pinus flexilis*), western yellow pine (*P. ponderosa*), and aspen (*Populus tremuloides*). Approximately 78 per cent of the larger-sized trees, over 6 inches in diameter, were Douglas fir, while only 29 per cent of the smaller trees were of this species, indicating a gradual replacement of the fir by the spruce and a general tendency toward an ultimate spruce type. The soil on the plots is a granitic gravel.

The four plots, arranged from west to east and separated by 40-foot isolation strips, were prepared as follows:

No. 1 was clear cut; No. 2 was left in its original condition to serve as a control, with 1,145 trees of Douglas fir, Engelmann spruce, limber and yellow pine, aspen, and willow (*Salix sp.*) of all ages comprising the stand; No. 3 was cut under the shelterwood plan, removing all but 83 of the thriftiest mature Douglas firs, which were well scattered over the area and in 1916 averaged 9.95 inches in diameter breast high; while plot No. 4 was cut as nearly under a selection system as the condition of the stand would permit. Two hundred and seventy-one Douglas firs were left, representing all sizes from 4½ feet high to mature trees. While the original stand was by no means even-sized, it was to a large extent even-aged, and many, if not most, of the small trees left were merely small through long suppression.

Following the cutting operation, all reproduction below 4½ feet in height was removed so as not to interfere with future counts.

In order to study the effect of different methods of slash disposal upon the character of the reproduction secured, the slash left after logging on the eastern half of each of the three cut-over plots was scattered over the ground, while that on the western half was piled and burned.

The first reproduction count was made in the year 1915, but was only partially completed because of the advent of bad weather. A complete count was made in 1916. No counts were made in 1917 and 1918, although casual observations during 1917 showed no new germination had come in, and that most of the 1916 germination had disappeared.

In the summer of 1919, a fairly complete study, including reproduction counts, tree measurements, the relation of brush, humus depth, grass, and root length to reproduction and survival, and observation of climatological conditions, was made and reported upon, and every fall since then reproduction counts have been made on 22 of the 20-by-20-foot sections located in diagonal strips across each plot, running S. 45° W. up the slope, and representing an average of all surface

[1] Received for publication June 19, 1924—issued Nov., 1924.

conditions. The actual area of each group of sections representing a certain method of treatment is 0.202 acre.

The total number of seedlings of the coniferous species present at each of the last 5 counts, on the basis of one acre, was as follows:

	Clear-cut	Control	Shelterwood	Selection
1919	1,287	9,009	4,035	3,352
1920	579	2,192	4,633	3,980
1921	1,083	3,826	7,028	6,465
1922	1,267	2,901	10,316	8,530
1923	1,569	3,821	13,427	9,707

It will be seen that since 1919 the selection and shelterwood areas have tripled the amount of reproduction, and that the clear-cut area is building up slowly, while the area under the original forest is showing no net increase. The extremely large number of seedlings present upon the control plot in 1919 was due to an exceptionally heavy crop of 1918 Engelmann spruce seedlings. Because of the presence of spruce seed trees upon the control plot this species is always well represented in the new crop of seedlings, considerably more so than on any other plot. In 1923, 42 per cent of the new control crop was spruce, while on the shelterwood and selection plots this species was present only to the extent of 6 and 2 per cent, respectively, and no new spruce seedlings at all were found upon the clear-cut area.

In each count the seedlings were tallied as new, 1 year old, 2 years old, and 3 years and older. The last class is considered established and is referred to as the "surviving" class. From a study of conditions on plot No. 3 in 1919, only approximately 6 per cent of the fir seedlings live after the first year. One-half of these die during the following three years, and more than likely most of them during the second year. The mortality rate after the third year is low.

SURVIVAL OF SEEDLINGS

Although it is always desirable to secure copious reproduction, the criterion of success for any system is the amount of survival, and it is in this respect that the virgin stand falls down. Fifty-nine per cent of all the reproduction present in 1923 on the control plot was represented by 1923 seedlings, of which the expectation of survival is very low. Under the shelterwood cutting all but 6 per cent of the trees were at least one year old, as was the case also on the clear-cut area, while in the selection forest only 1 per cent were new seedlings.

The following summary gives the number of established, or three-year-old, seedlings per acre for each system:

	Clear-cut	Control	Shelterwood	Selection
1919	287	238	811	480
1920	213	233	1,127	550
1921	881	2,271	5,004	3,985
1922	900	1,430	6,436	4,592
1923	1,005	1,237	6,891	4,638

Again, as in the case of total germination, there is a perceptible yearly increase on the cut-over plots. The big increase in 1921 is due to the 1918 Douglas fir seedling crop passing into the survival class. Under the virgin forest, the 3-year-old class is gradually decreasing, indicating that the seedlings are unable, even

after apparently becoming established, to combat the natural conditions under which they must grow.

It was found that only 32 per cent of the trees on the control plot in the 1923 count were 3 years and older, while on the selection plot these reached 48 per cent. Upon the shelterwood plot 51 per cent were 3-year seedlings, and 64 per cent upon the clear-cut plot.

The different species were represented in the 1923 surviving class by the following percentages:

	Clear-cut	Control	Shelterwood	Selection
Douglas fir	62	57	80.3	85
Engelmann spruce	20	36.5	19.2	12.7
Limber pine	18	6.5	0.4	2.1
Yellow pine	0	0	0.1	0.2

One object of the cutting experiment was to secure a young stand of Douglas fir to the exclusion of other species and, as will be seen, the shelterwood and selection plots have come closest to securing a fulfillment of this object. To a large extent, success in securing reproduction is dependent upon the seed supply, which has been abundant on all plots but the clear-cut. The high percentage of survival that this area shows indicates not so much growing conditions superior to the other areas as that little new reproduction is coming in. What does appear is mainly confined to the west (windward) and south sides of the plot, adjacent to heavy timber. It is evident that 1 acre is too large an area to be successfully reseeded from the sides when in the form of a square.

In general, the humus on the clear-cut plot is too deep to favor new reproduction, and an accumulation of new humus in the form of aspen leaves is beginning to cover the soil with a layer which seedling roots find it difficult to penetrate. The entire area is now covered with a heavy stand of aspen, some of which is 15 feet in height. While this is not so thick as through shade and moisture competition to preclude the possibility of fir reproduction, it is gradually building up such a barrier upon the ground as to offer serious hindrance to any reproduction that might appear despite the lack of seed.

The selection plot ranks low in percentage of spruce reproduction because it is the only treated plot having no spruce seed trees on its windward side. In general it has furnished as much fir reproduction as has the shelterwood plot, but it does not stand as high in survival of this species. It is quite possible that this is due to more favorable location of the shelterwood plot, as will be shown; but natural conditions of growth also favor the shelterwood plan in stands like this that are mostly even-aged.

MOISTURE A DETERMINING FACTOR

The results of several years' investigation of climatic factors upon the plots lead to the following interesting deduction regarding moisture supply: During the early part of the year moisture conditions are most favorable in the old-growth stand, where wind movement and insolation, the chief factors in evaporation, are at a minimum. The selection and then the shelterwood areas follow in order. Because of its exposure, the clear-cut plot shows the lowest percentage of soil moisture for the whole season. Since soil moisture appears to be a controlling factor in Douglas fir reproduction, any considerable amount of early germination on the clear-cut area is made difficult. However, there is less seasonal variation in moisture here and a more even supply than under any of the

other systems of treatment, on account of the small amount of tree growth. Thus it is that seedlings that get a start while stored-up moisture is available in the spring, and before the aspen activity starts, are furnished with a fairly uniform supply of moisture throughout the season and survive. This is in contrast particularly to the condition under the original stand, where the multitude of seedlings, accustomed at first to plentiful moisture, hence not stimulated to deep rooting, easily succumb as this moisture is rapidly exhausted by the roots of the older trees.

The shelterwood area, being protected by the control plot against excessive wind movement and evaporation, has practically as plentiful a supply of moisture in the spring as the selection plot with more crowns. This is due also to the accumulation of drifted snow in the winter along the west side, and a relatively small drain by the old trees, and insures good germination and survival. The factor of winter protection, provided by drifting snow and shelter from the control plot, is, however, a matter of relative position rather than one of the silvicultural systems involved. The prevention of drifting, on the other hand, especially on the clear-cut area, is a strong argument in favor of brush scattering.

But the moisture supply or lack of it, which is the determining factor in the success of reproduction, may in turn be determined by density of stand. The percentage of seedlings surviving is governed most directly by late summer or fall drought, which is most severe where the heaviest stand remains, in spite of the fact that the degree of protection of soil and seedlings varies with the density of the stand. All other conditions are inconsequential in comparison with the drought caused by the drain of the older trees upon the moisture near the surface. The seedling's worst enemy in many cases may be its parent tree.

The importance of soil moisture in the success of Douglas fir reproduction upon these plots was first brought out by F. B. Notestein in 1912. He established sixty 10-by-10-foot reproduction plots, regularly scattered over the entire area before it was cut, and studied the influence of light intensity, soil moisture at 1, 2, and 6 inches, organic content of the soil at 1 and 2 inches, and soil temperature at 6 inches, upon the character of the reproduction.

It was determined that Douglas fir will reproduce successfully in a light intensity of 8.5 per cent. In a stand having an average light intensity of 27.24 per cent, reproduction averaged most abundant at points of least light; but Notestein was satisfied this simply meant that there was sufficient light everywhere under such a stand, which is comparable to the present control stand, but that in the openings where light is intense other conditions were unfavorable.

Soil moisture was found to decrease with increase of light. At the same time, Douglas fir reproduction was greatest at those points having the greatest soil moisture. All facts indicated that soil moisture not only is a more potent factor than light in controlling reproduction, but that it is the controlling factor.

The total soil moisture varied directly with the amount of organic matter in the soil, while the available soil moisture varied inversely with it. The relation between the amount of humus and reproduction is uncertain, but the facts brought out indicate the probability that there is a point up to which humus increases water capacity more than wilting coefficient, and is, therefore, favorable to reproduction, and beyond which it has the reverse effect.

No relation was found between soil temperature and reproduction.

SLASH SCATTERING VERSUS SLASH BURNING

In order to compare the relative values of scattering slash and piling and burning it, the total Douglas fir, Engelmann spruce, and limber pine seedlings present in 1923 following the two methods of slash disposal are shown in Table I.

TABLE I.—*Effect of slash disposal on seedlings of various ages and species under different cutting systems*

Slash disposal and cutting methods	Number of seedlings remaining in 1923, by species and year of origin											
	Douglas fir				Engelmann spruce				Limber pine			
	1923	1922	1921	Older	1923	1922	1921	Older	1923	1922	1921	Older
Slash scattered:												
Shelterwood	901	267	5,465	5,009	30	20	277	825	00	40	0	30
Selection	1,277	297	2,455	4,287	50	0	89	356	20	20	0	129
Clear-cut	59	10	178	396	0	10	59	178	20	89	30	59
Total	2,237	574	8,098	9,692	80	30	425	1,059	40	149	30	218
Slash burned:												
Shelterwood	505	178	4,900	6,069	59	79	624	2,119	20	40	69	20
Selection	871	346	4,613	3,594	0	0	59	822	0	10	30	69
Clear-cut	109	20	446	851	0	0	30	228	10	20	40	297
Total	1,485	544	9,959	10,514	59	79	713	3,169	30	70	139	386

TABLE II.—*Effect of slash disposal upon all seedlings, all methods of cutting combined, expressed in percentage of survival*

Method of slash disposal and year of count	Percentage of survival of all seedlings by species			Percentage of survival of established seedlings (3 years old and over) by species		
	Douglas fir	Engelmann spruce	Limber pine	Douglas fir	Engelmann spruce	Limber pine
Slash scattered:						
1923 survival	48	28	41	48	25	36
1922 survival	48	28	38	48	25	33
1919 survival	51	28	35			
Slash piled and burned:						
1923 survival	52	72	59	52	75	64
1922 survival	53	72	62	52	75	67
1919 survival	49	72	65			

Since Douglas fir is the principal species and includes the bulk of the reproduction it may be said that the method of slash disposal plays a minor part in germination and survival. The results for all the counts so studied are very consistent. The fir, if anything, shows a very slight preference for the areas from which the slash has been removed by fire.

Engelmann spruce reveals a decided preference for slash-burnt areas, and a greater numerical survival there. This condition can be attributed largely to the fact that the cleared areas are more favorably located with reference to spruce seed sources. On a percentage basis this species survives somewhat better under slash, once it gets a start. The 1916 crop had 6.2 per cent surviving in the open in 1919, and 15.4 per cent under slash. This ratio may not be strictly representative, for the majority of years, but is credible in view of the rather slow rooting of spruce, its tolerance to shade, and a sensitiveness to high temperatures, which equals though it does not exceed the sensitiveness of Douglas fir.

Limber pine exhibits a preference for the open both for germination and for survival, which is in keeping with the tree's general demand for open conditions, and its habit of thriving in exposed locations.

Summarizing it may be said for all species that the method of slash disposal plays a minor part in germination and survival. Nor can the amount of slash scattered over the area be considered a criterion of the amount of immediate protection offered by logs, stumps, juniper, grass, twigs, and small litter, which furnish the seedlings protection through the critical period of the third year, when there is greatest danger from direct insolation. Again, although scattered slash effectively prevents grasses coming in after opening up the stand, nothing discovered in this study has indicated that grasses are detrimental to fir reproduction; on the contrary, it has been found that the seedlings prefer to a surprising extent the protection offered by grasses. The number of survivors found and their general thrift indicate that the losses here are no greater than under slash.

In 1919, 85 per cent of fir and 80 per cent of spruce had come up under immediate protection, irrespective of cleared and slash areas; in 1922 these figures were 87 and 82 per cent, respectively. Evidently fir takes advantage of cover more than spruce does. Healthy 1917 and 1918 fir seedlings were more abundant under slash in 1919, while healthy spruce of the same age was more abundant in the open. This is attributed to the fact that the humus under slash is a trifle too deep for spruce. However, both species show the best thrift under protection, as defined above. As a whole, the seedlings naturally had more chance to come up near protection upon areas where the slash had been scattered, but the difference was not a great one.

HUMUS DEPTH AND ROOT LENGTH

Though the principal factor in germination will be found to be moisture supply, survival is dependent to a great extent upon humus depth. There exists a definite relationship between drought and depth of humus and also between tolerable depth of humus and immediate protection. Protection permits about one-half inch of additional humus for fir, and less for spruce. A protected seedling may survive the first and crucial season in humus in which an unprotected one would succumb.

Since humus depth is important in governing the distribution and survival of fir and spruce seedlings, root length is of prime importance. The root must be able to push through the comparatively open, quickly desiccated layer of humus and secure a hold in the mineral soil beneath, where, if the seedling is to survive its first drought period, it must depend upon a more or less steady moisture supply.

A study of root length in relation to humus depth was made in 1919. Only a limited number of trees were studied, but enough, it is believed, to reflect the general trend of the relationship. The following figures represent seedlings about one year old:

DOUGLAS FIR

	Average root length	Average depth of humus
	Inches	*Inches*
Vigorous	3.94	0.81
Wilted	2.74	1.58
Dead	2.82	2.40

Average root length 2.75 inches.

ENGELMANN SPRUCE

Vigorous	2.75	1.18
Wilted	2.08	1.04
Dead	1.51	1.71

Average root length 1.80 inches.

Fir seedlings wilt with a difference of 1.16 inches in root length over humus depth, while the difference between vigorous seedling roots and humus depth is 3.13 inches. This would indicate a maximum depth of humus of between 1.50 and 1.75 inches for vigorous fir seedlings under protection, and 1 to 1.25 inches in the open. Spruce seedlings wilt with a difference of approximately 1.04 inches in root length, the difference for vigorous seedlings being 1.57 inches. Thus the maximum humus depth for vigorous seedlings will be about 1.4 inches. Without protection this figure will be about 1.1 inches.

The average humus depth in inches over the plots in 1919 was:

	Slash scattered	Slash piled and burned	Average
Clear-cut	1.90	1.20	1.55
Original forest			1.18
Shelterwood	1.30	.75	1.02
Selection	1.25	.77	1.01

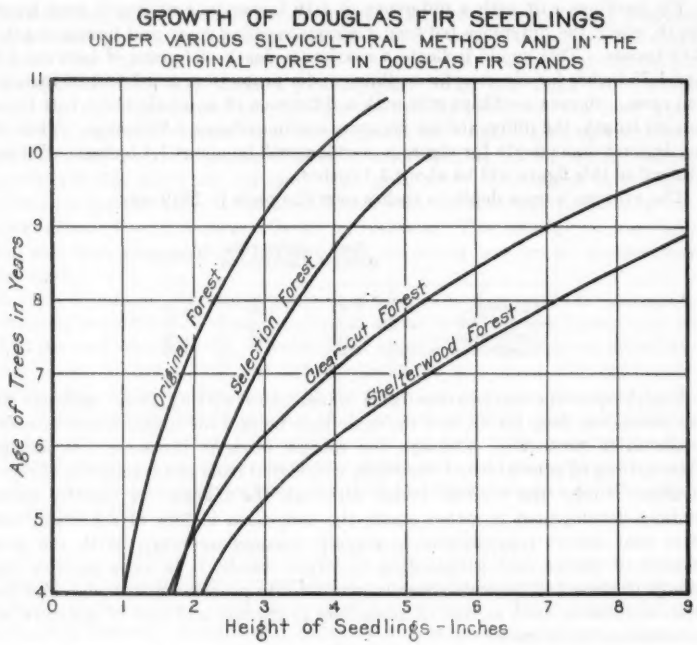
Except upon the slash-covered area under clear cutting, in no instance was the humus too deep for fir, and the same may be said for spruce where offered a modicum of protection, although the margin in most instances was smaller. Clear cutting in general is not desirable, considered from the standpoint of reproduction. Under the original stand, although the margin for healthy spruce seedling development is rather small, the long-term history of the stand indicates that spruce reproduction is actually favored over fir. With the great number of spruce seed germinating in virgin stands, it is quite possible that enough of these find favorable humus conditions to provide replacement, and that other conditions, such as lack of immediate protection and lack of moisture, act unfavorably upon the fir.

HEIGHT AND PROTECTION CORRELATED

When all species were grouped as protected and unprotected, it was found that protected seedlings are uniformly taller than those unprotected, this being more true of fir than of spruce. The average difference for fir is 0.27 inch, while for the spruce it is only 0.02 inch; but this latter figure is misleading due to an apparent reversal of form of the selection seedlings, which were 0.45 inch taller when unprotected. In every instance, the humus is from 0.3 to 0.6 inch deeper for protected fir and spruce seedlings. Although no measurements of root lengths were made, it is hardly likely that humus depth has any influence upon survival after the third year. However, assuming that the humus has increased in depth only a little since the advent of the seedlings, the favorable effect of protection combined with relatively shallow humus is evident.

It is not known at what rate humus has accumulated upon the plots since the original measurements were made, although it is reasonably certain that the heavy stand of aspen upon the clear-cut plot is having the effect of building up the humus layer and making it more difficult for seedlings to get started. This may also be the case upon the scattered-slash areas of the selection and shelterwood plots, but the young stand which has already established itself here makes it unnecessary to give any more consideration to the character of the humus.

An effort has been made in figures 1, 2, and 3 to illustrate the trend of height growths for Douglas fir, Engelmann spruce, and limber pine seedlings beginning with the fourth year, under the various methods of cutting and under the original stand. Insufficient data were at hand to construct a curve for limber pine on the shelterwood area, but the curves that are shown emphasize the superior per-


GROWTH OF DOUGLAS FIR SEEDLINGS
UNDER VARIOUS SILVICULTURAL METHODS AND IN THE ORIGINAL FOREST IN DOUGLAS FIR STANDS
Age of Trees in Years
Height of Seedlings - Inches
Original Forest
Selection Forest
Clear-cut Forest
Shelterwood Forest
0
1
2
3
4
5
6
7
8
9
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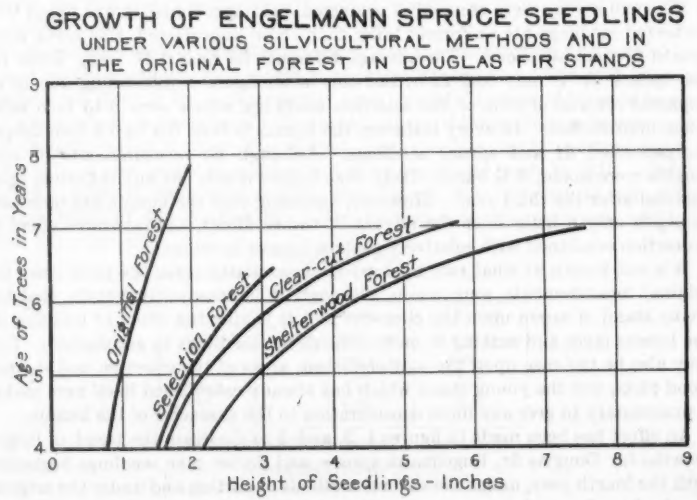
10
11

FIG. 1


GROWTH OF ENGELMANN SPRUCE SEEDLINGS
UNDER VARIOUS SILVICULTURAL METHODS AND IN THE ORIGINAL FOREST IN DOUGLAS FIR STANDS
Age of Trees in Years
Height of Seedlings - Inches
Original Forest
Selection Forest
Clear-cut Forest
Shelterwood Forest
0
1
2
3
4
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6
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8
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4
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FIG. 2

formance of Douglas fir and Engelmann spruce seedlings upon the shelterwood plot. In every instance, the clear-cut, selection, and original stands rank in order downward for each species.

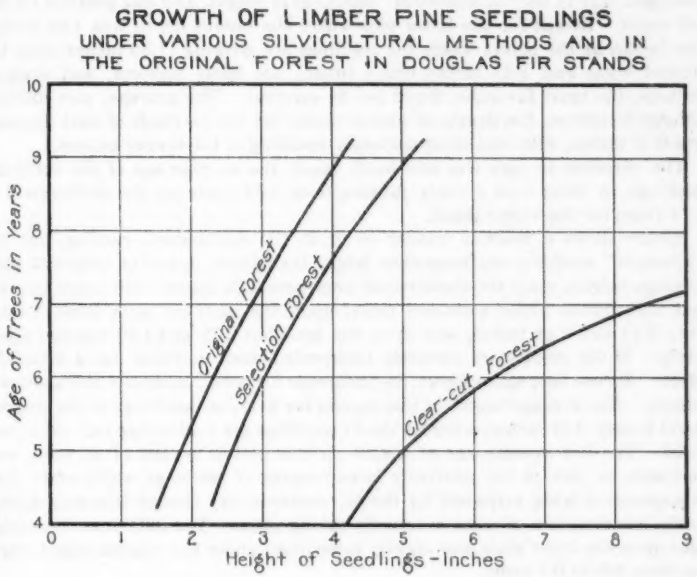

FIG. 3

SUPERIORITY OF SHELTERWOOD

For the past few years, the most striking fact noted in connection with the reproduction upon the plots has been the superior development of the young trees under the shelterwood cutting. This good growth is not confined to any one section or sector, but characterizes the young trees of both Douglas fir and Engelmann spruce over the entire area. It is rather difficult to place the responsibility for this better development upon any of the conditions which establish this plot as superior to the selection plot. In order to determine the relation between growth rates under the various methods of treatment, the seedlings on at least one half of the sections of each plot and all of them upon the clear-cut plot were measured in 1923. At the same time, the depth of humus was measured as near each seedling as could be done without disturbing the young tree, and the age of each tree was also determined.

On both slash-scattered and slash-burned areas under the shelterwood cutting, the Douglas fir seedlings averaged larger than on any of the other plots. Upon the slash-scattered area their average height was 3.53 inches, as against 2.66 inches for the clear-cut area, and 2.15 inches for the selection. Upon the slash-burned area, the respective heights in the same order were 3.12, 2.70, and 2.70 inches. The average height of fir seedlings under the old stand was but 1.49 inches. These figures represent groups varying from 40 to 341 seedlings, with average ages varying from 5.40 to 6.05 years and uniformly greater upon the slash-scattered areas. Curiously, the seedlings under slash on the shelterwood plot were larger than those under piling and burning, which was not the case with the selection

and clear-cutting systems. Humus depth, which does not represent the average depth to be encountered upon the various plots, and, therefore, can not be compared with previous measurements, was least for the "clear-cut" seedlings, which averaged next to the "shelterwood" seedlings in height, and was greatest for the old stand. Except for the latter plot where the humus depth was 1.93 inches, the depths at the points where the seedlings are growing (1.30 inches upon the cleared areas and 1.65 inches under brush) are fairly uniform, and suggest, perhaps, the most favorable depth for fir survival. The average, also uniform difference between the depths of humus under the two methods of slash disposal, was 0.35 inches, with scattering naturally resulting in the deeper humus.

The variation in ages was also fairly small, the average age of the surviving seedlings, or those over 3 years, ranging from 5.52 years for the shelterwood to 5.74 years for the virgin stand.

Spruce shows a reaction similar to fir in the shelterwood cutting, but the "selection" seedlings are somewhat larger than those upon the clear-cut plot. Average heights upon the shelterwood area were 3.26 inches with slash burning and 3.21 inches under scattered slash; upon the clear-cut area these heights were 2.13 and 2.18 inches, and upon the selection 2.78 and 1.79 inches respectively. If the results are correctly interpreted, slash burning has a beneficial effect. Spruce here again shows its preference for open conditions and shallower humus. The average height of this species for five-year seedlings in the original stand is only 0.97 inches, whereas the fir seedlings are 1.49 inches tall but a year older. The low average age of spruce on this plot is typical of all plots, and indicates, in view of the relatively large number of seedlings which start, that this species is being surpassed by the fir, contradictory though this may appear to the common idea of what is actually taking place. The difference in average ages upon the other plots was slightly lower than under the original stand, varying from 0.4 to 0.7 years.

Limber pine seedlings are much larger upon the shelterwood (6.60 inches under brush and 6.40 inches in the open) and clear-cut areas (7.63 and 6.95 inches) than upon the others (3.15 and 5.22 inches for the selection and 2.56 inches under the original forest), but show no decided preference for either method of slash disposal. The average age of these trees, 6½ years, shows that little new reproduction of this species is coming in. Practically all of the reproduction can be traced to seed originally stored in the duff or cached by squirrels.

This study of reproduction under the various cutting methods in Douglas fir stands has brought out the desirability of the shelterwood system, as particularly adapted to Douglas fir stands. It has not proved that slash scattering, employed mainly to furnish shade for the seedlings and help conserve soil moisture, has any decided silvicultural advantages over piling and burning of slash, save that it is the less expensive and therefore more desirable method. This is more or less a question to be decided upon the ground. The natural debris resulting from logging operations should ordinarily furnish all the protection the seedlings will need.

The success secured in regenerating under shelterwood and to a great extent under selection cutting is so obvious that it is now planned to make the second cut on the shelterwood stand within the next two years. Periodic reproduction counts will no doubt be continued, to show the effect of this final cutting and the course of development in the other plots.

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PLATE 1.

Shelterwood cutting, looking west through center of plot toward the uncut stand in control plot.

THE ISOLATION AND IDENTIFICATION OF QUERCETIN FROM APPLE PEELS[1]

By CHARLES E. SANDO

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Some time ago the writer's interest in possible relations between chemical constituents of the apple and storage scald in this fruit led to an investigation of the nonvolatile waxlike substances covering the epidermis.[3] This work has been extended to include a study of the yellow flavonol pigment which occurs in apple peels. The present paper deals with the isolation of the pigment and with its identification as quercetin, a widely distributed member of the flavonol group.

The isolation of quercetin has previously been reported from apple bark,[4] but no mention has hitherto been made of its occurrence in the peel of the fruit.

PREPARATION OF QUERCETIN

The material employed in this work consisted of peels of the McIntosh apple. It was obtained as a by-product in the investigations of Power and Chesnut [5] on the odorous constituents of apples. In their work, the fresh parings were subjected to distillation in a current of steam. The residue from the steam-distillation was used for the preparation of the flavonol. On account of this treatment and the necessity of prolonged extraction with alcohol, in the presence of malic acid contained in the parings, the glucoside of the flavonol was not obtained.

The wet peels after steam distillation were carefully dried and coarsely ground for purposes of extraction. The extractions were carried out by using a continuous extraction apparatus based on the Soxhlet principle. With this apparatus it was possible to extract about 1 kgm. of material at each loading. The dried material was first extracted separately with petroleum ether and ether in order to remove chlorophyll, carotinoids, and waxlike substances. These extractions were followed by the use of 95 per cent alcohol, which dissolved the coloring matter. The extraction with alcohol was continued for several weeks before the last traces of flavonol pigment were removed from the peels. After evaporation to eliminate the greater portion of alcohol, hot water was added to the syrupy residue. The liquid, upon the addition of neutral lead acetate solution yielded a precipitate which contained very little of the pigment. The lead precipitate was filtered off by means of a Buchner funnel and then basic lead acetate solution added to the filtrate. The basic lead acetate precipitate, which contained most of the coloring matter, was separated by filtration and decomposed by boiling with 5 per cent sulphuric acid. After removal of lead sulphate and cooling, the acid solution was repeatedly shaken with ether in a separatory funnel. Evaporation of the ethereal liquid left a residue consisting of crude

[1] Received for publication May 21, 1924—issued Nov., 1924.

[2] In connection with this work thanks are given to Dr. Frederick B. Power for his kindness in supplying the material employed.

[3] SANDO, C. E. CONSTITUENTS OF THE WAX-LIKE COATING ON THE SURFACE OF THE APPLE. Jour. Biol. Chem. 56: 457–468. 1923.

[4] ROCHLEDER, F. QUERCITRIN AND QUERCETIN. Jahresber. Fortschr. Chem. 1867: 731–732. 1869.

[5] POWER, F. B., and CHESNUT, V. K. THE ODOROUS CONSTITUENTS OF APPLES. II. EVIDENCE OF THE PRESENCE OF GERANIOL. Jour. Amer. Chem. Soc. 44: 2038–2042. 1922.

coloring matter which weighed 2.45 gm. in the air-dried state. This quantity of impure pigment was obtained from 68.6 kgm. of fresh skins, which represented 545.7 kgm. of whole apples. After purification of the crude material only about 0.5 gm. of pure pigment remained.

IDENTIFICATION OF QUERCETIN

Acetylization of the unidentified substance was carried out by boiling the impure pigment with anhydrous sodium acetate and acetic anhydride. The reaction mixture was poured into water and set aside over night. The product thus obtained, after several recrystallizations from 70 per cent alcohol, amounted to 1.15 gm. It consisted of a feltlike mass of colorless needles which melted at 194° to 196° C. When the substance was mixed with pure authentic penta-acetylquercetin its melting point was not altered. The substance was thus identified as penta-acetylquercetin. Combustion of the anhydrous compound dried at 160° confirmed this conclusion.

0.1489 gm. gave 0.3196 gm. CO_2 and 0.0531 gm. H_2O.

Found: C = 58.53, H = 3.99.

Acetylquercetin, $C_{15}H_5O_7(C_2H_3O)_5$, requires: C = 58.57, H = 3.93.

From the penta-acetylquercetin the free pigment was regenerated by hydrolysis with a few drops of sulphuric acid in glacial acetic acid. After boiling a few minutes, the mixture was well diluted with water and set aside in the ice box for several days. The insoluble compound was collected in a weighed Gooch crucible and dried at 130°.

0.8436 gm. gave 0.4984 gm. recovered pigment.

Found: Pigment = 59.08.

Acetylquercetin, $C_{15}H_5O_7(C_2H_3O)_5$, requires: $C_{15}H_{10}O_7$ = 58.98.

The substance obtained by regeneration from its acetyl derivative responded to all the tests of pure quercetin. Crystallized from dilute alcohol, it formed a glistening mass of yellow needles which were almost insoluble in water, but readily soluble in alcohol. Solution in dilute alkalies intensified the yellow color. With alcoholic ferric chloride it gave a dark-green color. When reduced in alcoholic solution with magnesium ribbon and hydrochloric acid it developed a characteristic bright red anthocyanic color. Analysis of the substance, dried at 130°, showed that it agreed in composition with quercetin.

0.1559 gm. gave 0.3399 gm. CO_2 and 0.0466 gm. H_2O

0.1325 gm. gave 0.2891 gm. CO_2 and 0.0379 gm. H_2O

Found: C = 59.46, 59.50; H = 3.35, 3.21

Quercetin, $C_{15}H_{10}O_7$, requires: C = 59.59, H = 3.34.

DISCUSSION

There is some reason for assuming that quercetin in apple peels may be the chromogenic substance which is responsible for the formation of brown pigment of scalded apples. The investigations of Nagai[6] have shown that the color of aqueous or alcoholic extracts of numerous plant tissues rich in flavones changes to brown or reddish-brown when the extracts are treated with freshly prepared plant juice containing oxidizing enzyms. This color transformation is attributed to the oxidation of certain flavone and flavonol pigments or their glucosides and in accordance with this view Nagai has shown that chemically pure preparations of the pigments themselves yield brownish colors by the action of enzyms. For example, the addition of oxidase to quercetin resulted in the development of a

[6] NAGAI, I. A GENETICO-PHYSIOLOGICAL STUDY ON THE FORMATION OF ANTHOCYANIN AND BROWN PIGMENTS IN PLANTS. Jour. Col. Agr. Imp. Univ. Tokyo 8:1-92, illus. 1921.

deep red color which rapidly changed to brown. Quercitrin, a monorhamnoside of quercetin, under the same conditions yielded a less bright red color than quercetin. It was shown that the brown pigment developed at the expense of flavonol or its glucoside in solution. These results with quercetin or its glucoside and oxidase suggest that the brown pigment appearing in scalded apple peels may be produced by interaction in the tissues of quercetin and oxidase which are normally present in the skin. The observation that brown discoloration of scalded peels is more prevalent on the greener portions lends support to the possibility of quercetin or its glucoside being the parent substance of the brown pigment. The bright-red areas are highly resistant to scald and there is reason for believing that flavonol occurs in smaller quantities in these localities because of its conversion into red or anthocyanic pigment.

It should be borne in mind, however, that other substances in the apple may play a part in the formation under certain conditions of brown or reddish brown color. According to Overholser and Cruess [7] the darkening of cut surfaces of apple tissue may be due to the oxidation of a tannin-like substance. It is interesting to note in this connection that flavonols and tannins are built up of similar nuclei and hence may yield closely related brown products on oxidation.

SUMMARY AND CONCLUSIONS

(1) One of the first indications of scald in apples is the appearance on the greener portions of the fruit of a typical brown discoloration. A possible relation between the suspected occurrence of a flavonol pigment in the skin and scald led to the isolation and identification of this pigment.

(2) The particular flavonol coloring matter, which was found to occur in McIntosh apple peels, proved to be quercetin, $C_{15}H_{10}O_7$. It was identified by means of its penta-acetyl derivative and by combustion of the purified pigment itself.

(3) It is suggested, as a basis for further investigation, that quercetin, or its glucoside which has not been isolated, may be the chromogenic substance which is responsible for the formation of brown pigment in the peels of scalded apples.

[7] OVERHOLSER, E. L., and CRUESS, W. V. A STUDY OF THE DARKENING OF APPLE TISSUE. Calif. Agr. Exp. Sta. Tech. Paper 7: 40 p. 1923.

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GAMETE PRODUCTION IN CERTAIN CROSSES WITH "ROGUES" IN PEAS [1]

By WILBER BROTHERTON, Jr.

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The inheritance of the narrow, pointed stipuled mutation or "rabbit-eared" rogue in garden peas, *Pisum sativum* L., is unusual. Bateson and Pellew [2] found that in crosses with the parent, or broad, obtusely stipuled type, the rogue character is dominant, and that in the F_2 and succeeding generations only rogues appear. There is a failure of the expected segregation into rogue and type plants.

Besides the extremely narrow and the very broad stipuled plants, the same authors [3, 4] described certain intermediate forms which on self-fertilization give varying proportions of rogues, intermediates, and types in their progenies. Intermediates showing a high percentage of rogues among their offspring showed a progressive increase in the percentage of rogues to nonrogues among their progeny when comparing plants derived from the lower nodes with offspring from the upper nodes of the same intermediate plant. The change in ratio between the two classes of plants was accounted for by a corresponding increase among the male gametes of those bearing the rogue factors. The authors point out an association between the excessive production of rogues in the F_1 hybrids and the progressive change in the numerical proportions of rogues to types in the progeny of intermediates on the one hand with a progressive change during growth from type to rogue, in the somatic appearance of both the F_1 hybrids and the intermediates on the other.

In 1923 [5] the writer reported the fact of segregation in the F_2 generation of crosses between Gradus rogue and typical plants of Mummy, a nonrogue-producing variety of peas. Although both rogues and nonrogues appeared in the F_2 and F_3 generations of this cross, the ratio between the two classes of segregates did not accord with any known Mendelian system. The rogues greatly outnumbered the nonrogues. The F_1 hybrids resembled in their genetic behavior the intermediates described by Bateson and Pellew, but no data were secured as to the character of the progeny at successive nodes or of the actual ratio of rogue to nonrogue gametes among the ovules and pollen grains.

From the facts obtained, the hypothesis was advanced that rogues arise *de novo* from the parent type by mutation of a single factor, x to X. It is believed that the heterozygous Xx combination is very unstable. In the presence of X

[1] Received for publication April 12, 1924—issued Nov., 1924.

[2] BATESON, W., and PELLEW, C. ON THE GENETICS OF "ROGUES" AMONG CULINARY PEAS (PISUM SATIVUM). Jour. Genetics 5:13-36, illus. 1915.

[3] BATESON, W., and PELLEW, C. NOTE ON AN ORDERLY DISSIMILARITY IN INHERITANCE FROM DIFFERENT PARTS OF A PLANT. Proc. Roy. Soc. [London] (B) 89: 174-175. 1916.

[4] ——— THE GENETICS OF "ROGUES" AMONG CULINARY PEAS (PISUM SATIVUM). Proc. Roy. Soc. [London] (B) 91: 186-195. 1920.

[5] BROTHERTON, W. E., JR. FURTHER STUDIES OF THE INHERITANCE OF "ROGUE" TYPE IN GARDEN PEAS (PISUM SATIVUM L.) Jour. Agr. Research 24: 815-852, illus. 1923.

the factor x mutates readily to X during somatic development so that at gametogenesis the F_1 hybrid of type with rogue is homozygous for the rogue factor.

The allelomorphe of X in Mummy is called x′ and differs from x of the rogue-producing variety in being more stable, rarely, if ever, mutating to X when in the homozygous x′x′ condition. However, in the heterozygous Xx′ combination (F_1 and succeeding generations of rogue × Mummy) the combination, while more stable than the Xx germplasm of rogue × type, nevertheless is fairly unstable, and x′ mutates frequently to X. The frequent change of x or x′ to X during development of the plant is called mass somatic mutation and the unequal proportion of the two kinds of gametes formed, that is, x or x′: X, results in masking the true Mendelian nature of the inheritance.

The behavior of certain atypical F_1 hybrids of the same cross indicated that occasionally x and x′ mutate to produce intermediate forms in regard to stipule shape. The inheritance of these latter forms has not been studied.

Since the assumed genetic constitution of the rogue, type and Mummy was derived from the fact of segregation rather than from the actual F_2 ratios observed, it seemed desirable to analyze further the character of the gamete production by the F_1 hybrid of rogue crossed with a nonrogue-producing variety. When out-crossing such an F hybrid with Gradus type, a rogue gamete uniting with a type gamete would produce a rogue, and a nonrogue gamete uniting with a type gamete would produce a nonrogue plant. This paper is a preliminary report of the results of such an analysis.

The F_1 plants of rogue × Mummy are very late in flowering and therefore difficult to cross with the early-flowering Gradus type. For this reason the F_1 plants of rogue × Rice's 330 (a nonrogue-producing variety) were substituted. Rice's 330 is an early-maturing sort with stipules intermediate in size and shape between Gradus type and Gradus rogue. The mean ratio of $\frac{\text{length of stipule}}{\text{width of stipule}}$ as determined by measurements of four stipules from the upper part of mature plants for the three parental types was as follows: Gradus type, 1.693±0.0107; Gradus rogue, 2.339±0.0096; and Rice's 330, 1.991±0.0086 (Table I).

In 1919, 36 F_1 hybrids of Gradus type × Rice's 330 were grown and found to have a mean stipule ratio of 1.825±0.0098, i. e., intermediate between the two parents (Table I). The stipules were larger than those of Rice's 330 and narrower than Gradus type, but had the emarginate apices typical of Gradus rather than the more acutely pointed stipules of Rice's 330.

During the summer of 1920, the writer was unable to have stipule measurements taken until very late in the season, at which time the foliage of only a few of the late flowering segregates was still green enough to measure. In all 87 plants from 21 families were measured. The mean, standard deviation, and coefficient of variation are given in Table I.

The F_2 segregates were not classified by inspection, and since the data are meager, no attempt is made to analyze the factorial differences between the two parents. The data are given at this time merely for comparison with that which follows.

The F_2 hybrids of Rice's 330 × Gradus rogue and reciprocal, 32 in all, grown in 1919, were intermediate between Rice's 330 and Gradus rogue in appearance, with a mean stipule ratio of 2.185±0.0213 (Table I).

The F_2 generation consisted of 47 families, from which the mean stipule ratios of 247 plants were obtained. The range of variation includes that of both parents and indicates segregation into rogue and nonrogue forms (Table I). No data are available as to the exact segregation, since the plants were not classified by stipule shape.

TABLE I.—*Frequency distributions and statistical constants for ratio of* $\frac{\text{length of stipule}}{\text{width of stipule}}$ *for Gradus type, Gradus rogue, Rice's 330, and various F_1 and F_2 hybrids, and back-cross segregates*

	1.35	1.45	1.55	1.65	1.75	1.85	1.95	2.05	2.15	2.25	2.35	2.45	2.55	2.65	2.75	2.85	2.95	Total	M.	σ	C. V.
Gradus type (P_1)	1	0	16	64	33	18	3											135	1.603+0.0107	0.098+0.0075	5.78+0.2381
Gradus rogue (P_1)								7	21	33	30	22	10	8	4			135	2.339+ .0096	.165+ .0068	7.06+ .2912
Rice's 330 (P_1)					3	9	17	27	7									63	1.991+ .0086	.101+ .0060	5.07+ .3504
F_1 (Gradus type × Rice's 330)				1	14	15	6	1										36	1.825+ .0098	.088+ .0069	4.82+ .3832
F_1 (Gradus rogue × Rice's 330)			1	8	14	22	21	12	5	4								87	1.899+ .0113	.157+ .0080	10.44+ .4931
F_2 (Gradus rogue × Rice's 330)						3	1	6	6	7	6	3						32	2.185+ .0213	.179+ .0151	8.19+ .6950
F_1 (Gradus rogue × Rice's 330) × type, all segregates					2	11	16	26	21	28	48	50	30	24	13	8	1	278	2.350+ .0101	.081+ .0046	4.63+ .2664
F_1 (Gradus rogue × Rice's 330) × type, nonrogue segregates		3	13	38	14	10	12	13	11	12	7	2	1	2				138	1.975+ .0159	.278+ .0112	14.07+ .5794
F_1 (Gradus rogue × Rice's 330) × type, rogue segregates		3	13	38	13	2												69	1.748+ .0065	.081+ .0046	4.63+ .2664
					1	8	12	13	11	12	7	2	1	2				69	2.223+ .0155	.192+ .0110	8.63+ .4622

However, some idea of the character of the F_2 segregation following the cross between rogue and Rice's 330 may be obtained from a classification of 262 F_2 plants grown in 1923 from 5 F_1 hybrids grown in 1922 under a wire cage to protect them from volunteer crossing by insects. The F_2 plants were grouped as rogues, intermediates with pointed stipules of greater width than in typical rogues, and as broads with large stipules resembling Rice's 330 or Gradus type. The variability of the rogues and intermediates was such that it was not always easy to separate them, but the differences between the two roguelike classes and the broads or type-like plants were easily recognized. In all there were 217 rogues, 37 intermediates, and 8 broads, clearly not a typical Mendelian segregation.

During the winter of 1922–23 there were grown 155 plants from 32 back-crosses of the kind [(rogue × Rice's 330) × type], as well as 8 of the reciprocal back-crosses. The F_1 hybrids used as either pollen or pistillate parents were the same 5 plants whose F_2 progeny, derived from self-fertilized seed, were grown in 1923 and described above.

The progeny of these back-crosses were for the most part easily distinguished as broads with wide, rounded stipules, or as rogues with characteristic narrow, pointed stipules. The stipule differences between these two classes of segregates is clearly shown by the data for their mean stipule ratios given in Table I. The frequency distribution and mean of 1.748 ± 0.0065 for the broad segregates are very near those of the F_1 hybrids of Rice's 330 × Gradus type. The variability in stipule shape among the broad segregates, as shown by the coefficient of variation, is also strikingly near that of the F_1 generation of the latter, i. e. $4.63 + 0.2664$ and $5.07 + 0.3054$, respectively.

The narrow or roguelike segregates resemble closely the pure rogues in regard to their frequency distribution, except that the range of variation of the hybrids extends below 2.05, the lowest class of pure rogues. The mean, 2.223 ± 0.0155, is significantly different from that of 2.339 ± 0.0096 for the pure rogues, but is also decidedly different from that of the broad (nonrogue) segregates.

The roguelike plants also resemble the rogue parent in the great variability they exhibit, caused in part by the presence of chimeralike segregates characterized at the middle and upper nodes by having the corresponding stipules of each pair unlike, that is, one stipule narrow and pointed while the other stipule would be broad and obtuse. In all, 13 chimeras were identified, 10 from seed pollinated by the type and 3 from the reciprocal cross. The following measurements of the stipules at successive nodes are typical of this class. The ratios for the pair of stipules from the same node are inclosed in brackets and the largest ratio, usually above 2.05, indicates in every instance the roguelike stipule.

Plant No.	3.100-2	3.111-2	3.118-1
	(1.71)	(1.66)	(1.86)
	(2.76)	(1.81)	(2.55)
	(1.87)	(1.63)	(1.55)
	(3.36)	(2.33)	(2.77)
	(1.53)	(1.82)	(1.92)
	(2.09)	(2.36)	(2.66)
Average	2.05	1.93	2.21

In the data given in Table I the chimeras are classed as rogues, presumably heterozygous for the rogue factor, as shown by the presence of both the pointed and obtuse stipules. Whether the chimeras are merely heterozygous forms or are mosaics in the sense of Bateson and Pellew is not known, since each plant produced only two or three seeds in the greenhouse, and these too late for spring planting.

It is hoped to have data soon on the genetic behavior of comparable material from similar back-crosses made during the past summer.

The classification of the F_2 segregates according to their nodal origin from the F_1 hybrid is shown in Table II. There is a slight tendency for the proportion of rogues to nonrogues (broads) to increase toward the upper nodes, but as the total number is small, emphasis in the interpretation can not be put on this feature of the data. There may be an excess of nonrogue gametes produced by the ovules and an excess of rogue gametes produced by the pollen grains. However, the numerical differences between the two classes are slight enough to be well within the experimental error for so few plants if the real gametic ratio between the rogues and nonrogues was 1: 1, irrespective of which way the cross was made. The ratio of rogues to nonrogues for both crosses combined actually is 77: 78, or practically 1: 1.

On the other hand, the occurrence of a large number of rogues in the F_2 generation above the proportion theoretically expected for a monohybrid ratio can be explained by assuming the probable excess production of rogue-bearing male gametes indicated by the F_1 back-crosses actually occurred, especially at the upper nodes. The five F_1 plants used were exceptionally tall and flowered over a much longer period than the Gradus types. Consequently the back-crosses were made with flowers largely from the eighth to the fourteenth nodes of the hybrids. The self-fertilized plants came for the most part from the fourteenth to the twentieth nodes on the main stem, or from branches of the main stem produced late in the season.

From the foregoing it appears that the zygote heterozygous for the rogue factor is unstable. Apparently the presence of the rogue factor causes a change or mutation of the allelomorphic factor which entered the hybrid from Rice's 330. This genetic change during the development of the plant is most often due to the rogue factor itself, but occasionally it may take some other form, or the rogue factor itself may change. In either event a roguelike plant, possibly the F_2 intermediates or the chimeras here described, is the outward expression of the change.

A comparable case has been reported by Blaringhem [6], who studied the behavior of a mutation in Pisum with green cotyledons from a variety with yellow cotyledons. On self-fertilization the green-seeded peas gave varying proportions of plants with green, yellow, and variegated green and yellow seeds. The yellow seeds breed true, while the variegated and green seeds repeat the splitting. Seven self-fertilized green-seeded plants gave only green-seeded plants from the upper and lower nodes, while the middle nodes gave all three types. The totals for all seven plants were 118 green, 26 variegated, and 17 yellow. This author describes the phenomenon as one of hereditary mosaic, evidently believing that the green plants are a genetic mosaic of green and yellow and that "disjunction" of the two characters takes place under certain environmental conditions. He suggests that the manifestation of the true nature of the green-seeded plant or mosaic is dependent upon the age of the plant and the environment, especially temperature and humidity.

As Bateson and Pellew point out in discussing the genetic behavior of the intermediates they have described, where the gametic output is so fluctuating it is perhaps unwise to hypothecate a factorial system to interpret the results. Nevertheless, it is believed that here the presence of rogue and nonrogue gametes in the ratio of approximately 1:1, at the lower nodes at least of the F_1 hybrid between Rice's 330 and rogue, indicates a single-factor difference

[6] BLARINGHEM, L.—HÉRÉDITÉ ANORMALE DE LA COULEUR DES EMBRYONS D'UNE VARIÉTÉ DE POIS (PISUM SATIVUM L.). Compt. Rend. Acad. Sci. [Paris] 174:877-879. 1922.

between the two in regard to the rogue character. It would appear that subsequently the original 1:1 gametic ratio is disturbed by somatic mutation, so that from the upper nodes of the main stem and from its branches an excess of rogue gametes is produced. No attempt has been made to determine what external influences, if any, affect the gametic ratio.

TABLE II.—*Distribution according to nodal origin from the F_1 hybrid between Rice's 330 and rogue of self-fertilized progeny and of progeny derived from back-crosses with Gradus type*

	Hybrid ♀			Hybrid ♂			Self-fertilized			
	Non-rogue	Rogue	Ratio	Non-rogue	Rogue	Ratio	Non-rogue	Inter-mediate	Rogue	Ratio
8	4				2					
9	2	3	1:1.5	9	9	1:1.0			8	
10	3	3	1.0	2	9	4.5	2	1	15	1:8.0
11	12	5	0.4							
12	7	3	0.4				1		3	3.0
13	4	3	0.7					2	9	
14	9	8	0.9	2	4	2.0	1	2	8	10.0
15	6	9	1.5				1	3	10	13.0
16	4	7	1.7					6	7	
17	2	2	1.0				1	2	27	29.0
18		2						10	16	
19								1	15	
20								2	17	
5									4	
6								1	3	
7								2	3	
8								2	2	
9										
10	4	4	1.0						5	
12	2						2	1	4	2.5
13	1	3	3.0						5	
14									18	
15	4	2	0.5						11	
16								1	18	
17								1	5	
18									4	
Total	64	54	1:0.8	13	24	1:1.8	8	37	217	1:31
								254		

SURVEY OF BLISTER RUST INFECTION ON PINES AT KITTERY POINT, MAINE, AND THE EFFECT OF RIBES ERADICATION IN CONTROLLING THE DISEASE[1]

By G. B. POSEY, *Pathologist*, and E. R. FORD, *Assistant Pathologist, Blister Rust Control, Bureau of Plant Industry, United States Department of Agriculture*

PINE INFECTION SURVEY, 1916–1918

In 1916 an outbreak of white pine blister rust (*Cronartium ribicola*, Fischer) was discovered in the southern part of York County, Maine. Extensive scouting during the same season revealed the rust present in varying degrees of abundance throughout southern Maine and adjacent New Hampshire. The oldest and severest attacks of the disease found in these regions were upon stands of native white pine (*Pinus strobus*, L.) near a patch of cultivated black currants (*Ribes nigrum*, L.) at Kittery Point, Me. These currants had been brought from Nottingham, England, during the summer of 1897 and planted in a small garden surrounded by nearly pure stands of second growth white pine comprising mixed age classes. Systematic inquiry and search failed to show that any foreign white pine stock had been planted at or near Kittery Point, thus contradicting the supposition that the disease became established through that medium. The maximum ages of the more advanced rust lesions on pines in the immediate vicinity indicate that the establishment of blister rust at Kittery Point was coincident with the time when the patch of imported black currants was planted. This is further evidenced by the fact that the oldest pine infections found in that region are in the immediate vicinity of these currant bushes.

In 1917 approximately 6 square miles of the infested area at Kittery Point were included in an experimental local control tract on which both wild and cultivated currant and gooseberry bushes were located and uprooted by systematic crew work.[2] Before eradication began a 31.5-acre block surrounding the patch of imported black currants was plotted and each pine, currant, and gooseberry located for detailed investigation.

In 1918 careful studies were made of conditions on the 31.5-acre tract to determine the severity of infection on pines and other facts relative to the spread of the rust. Results of these investigations are shown in the charts and tables which accompany the following discussions.

DISTRIBUTION OF PINE INFECTIONS WITH RELATION TO THE PRESENCE OF RIBES AND THE INFLUENCE OF STORM WINDS

The effect of different patches of Ribes in causing blister rust infection on pines was evidenced by the condition of the trees and stands nearest these bushes. In cases where the Ribes had caused pine infection, the amount of infection on pines varied according to the species, size, and exposure of the Ribes and was greatest on near-by pines. In several instances the Ribes were small and densely screened and apparently had not caused pine infection. (See fig. 1.)

[1] Received for publication May 9, 1924—issued Nov. 1924.

[2] A crew consisted of 4 to 6 men in line, followed by a foreman. Intervals between line men varied according to the density of ground cover. In dense brush the interval was 6 feet or less while in open tracts the interval increased up to 20 feet. Efficiency was maintained by the constant checking of the foreman and by the crew systematically reworking definite units.

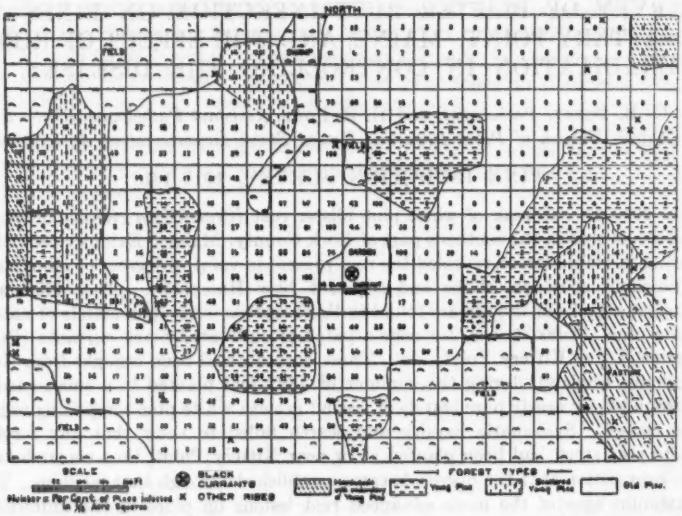

FIG. 1.—Compilation of data collected on the 31.5-acre experimental area in 1918. Each square represents one-sixteenth acre, and the numbers in the squares represent the percentage of pines infected when the pines were examined in detail in 1918.

INFLUENCE OF WIND

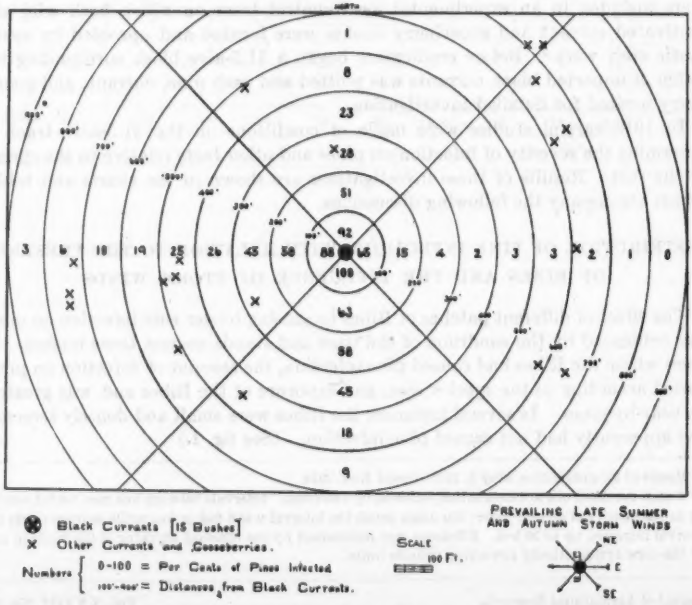

FIG. 2.—Data collected on the 31.5-acre experimental area. Figures represent per cent of infected pines in each quadrant by 100-foot zones.

The predominant effect of the patch of cultivated black currants in causing infection as compared to the possible effect of the other Ribes found on the area is shown in figure 2. The percentage of infected trees in concentric 100-foot zones from the black currants shows pronounced and fairly regular decreases in the four directions of the compass, whereas this would not be the case in similarly spaced zones circumscribing any other point as an infection center. The highest percentages of infection, when considered in relation to the location of the black currants, are in the paths of the late summer and autumn storm winds. On this basis, infection emanating from the patch of black currants was traceable in diminishing degrees for distances of 600 to 900 feet while infection from other Ribes was comparatively meager on nearby pines and not traceable beyond 200 feet.

RATE OF INFECTION OF STAND

The blister rust became measurably established on pines in the west half of the area studied at Kittery Point in 1901. From 1901 to 1916, inclusive, 34.5 per cent of the trees became infected. The rate at which the stand became infected increased from a yearly average of 0.225 per cent during the first 4-year period to a yearly average of 4.6 per cent during the last 4-year period preceding the eradication of Ribes.

TABLE I.—*Rate of infection of stand* [a]

	First 4-year period (1901–1904)	Second 4-year period (1905–1908)	Third 4-year period (1909–1912)	Fourth 4-year period (1913–1916)
Total number of healthy trees at beginning of 4-year period	6,727	6,666	6,317	5,386
Number healthy trees that became infected during the 4-year period	61	349	931	986
Per cent of healthy trees that became infected during 4-year period	0.9	5.2	14.7	18.3

[a] Table I is compiled from the data on the west half of the experimental area shown in Figure 1.

SEVERITY OF INFECTION ON PINES OF DIFFERENT SIZE CLASSES

The percentage of infection was lowest among trees of the smallest size and highest among trees of the largest size. Table II indicates that on the area studied the percentages of trees infected are correlative to their diameter-size classes.

TABLE II.—*Percentage of pines infected, by diameter classes* [a]

Diameter breast high	Number of pines	Trees infected	
Inches		*Per cent*	
1 and under	3,752	21	
2	700	34	37.3
3	412	43	
4	338	43	42.5
5	264	42	
6	165	61	57.5
7	160	54	
8	169	62	60.5
9	155	59	
10	149	71	65.8
11	130	60	
12	109	66	74.7
13 and over	224	79	

[a] Table II is compiled from the data on the west half of the experimental area shown in Figure 1.

SEVERITY OF INFECTION IN PINE STANDS OF DIFFERENT DEGREES OF STOCKING

In different units of the area, similarly exposed to Ribes, the percentages of infected trees varied according to the degrees of pine stocking. The percentages of infected trees were highest in understocked stands and lowest in overstocked stands. Figure 3 shows the percentages of trees infected in stands of the area having different degrees of pine stocking.

PINE INFECTION SURVEY, 1921

In 1921 an inspection was made of the entire experimental control tract at Kittery Point, where the Ribes eradication work had been done in 1917, to ascertain the effectiveness of this work in preventing further infection of the pine. No pine infection occurring since 1916 was found except in isolated portions of

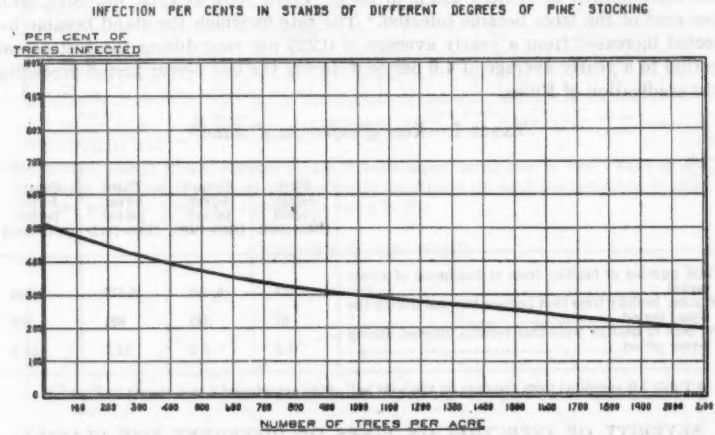

FIG. 3.—Compiled from the data on the west half of the experimental area shown in fig. 1

the tract where an occasional Ribes bush had been missed by the eradication crews or new ones had grown since 1917. Detailed investigations were made on thirty-two $\frac{1}{75}$-acre plots located in the experimental area where all of the Ribes bushes had been destroyed in 1917 and no new bushes had grown since that time, to determine the condition of the pines and the changes which had taken place in the stands.

On the 32 plots there remained 1,737 trees of the original stand studied in 1918 Of these, 31 per cent or 546 trees had been killed by the blister rust as a result of infections which occurred prior to the eradication of Ribes. Painstaking examination of the remaining 1,191 live trees of the original stand and 485 young trees that had seeded in on the area since 1917 showed that no new infections had occurred since 1916.

There was a marked variation in the severity of infection of different crown classes (fig. 4.) The dominant trees, which are of greatest economic importance in the stand, were subject to the highest degree of infection from blister rust.

SEVERITY OF BLISTER RUST INFECTION IN DIFFERENT CROWN CLASSES

PERCENTAGE OF PINES INFECTED BY CROWN CLASSES

FIG. 4.—A compilation of data for all trees on thirty-two $\frac{1}{4}$-acre plots located 100 to 400 feet from the site of the imported black currants in the west half of the area shown in fig. 1

CONDITION OF THE STAND

As shown in figure 5, there has been a constant increase in the number of trees dying from the effect of blister rust, while the number of infected trees has remained the same as in 1917. The number of healthy trees has been augmented by 485 young pines which seeded in during the four-year control period. This demonstrates that the destruction of Ribes prevented the occurrence of new infections and allowed pine reproduction to continue at an average annual rate of 60 trees per acre.

CONDITION OF STAND ON CONTROL AREA IN 1917 AND 1921

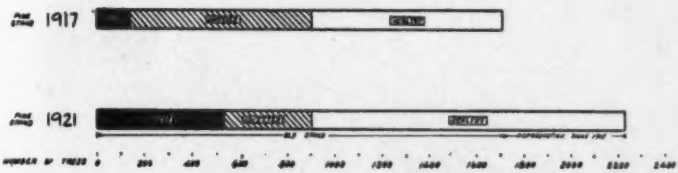

FIG. 5.—A compilation of data collected on the thirty-two $\frac{1}{4}$-acre plots described under fig. 4

SUMMARY

Investigations reported in this paper indicate that a patch of cultivated black currant plants introduced from England in 1897 and planted at Kittery Point, Me., during the same year, established a primary infection center of the white-pine blister rust whence the disease became widely spread through the neighboring white-pine forests. On the basis of detailed investigations conducted on experimental areas selected in and about the primary infection center, the following facts are evidenced:

1. Cultivated black currants were the Ribes mainly responsible for causing the pine infection on the area studied.

2. In cases where either wild or cultivated Ribes bushes had caused pine infection, the greatest amount of infection occurred in the nearest pine stands, and the infection from these bushes rapidly decreased at greater distances.

3. The highest degrees of pine infection were in the paths of late summer and autumn storm winds.

4. The average annual rate at which the pine stands became infected constantly increased over a period of 16 years and in 1916 the rate of infection was 20 times the rate in 1901.

5. The infection percentages in pine stands varied according to the diameter classes of the trees, being highest among the larger size classes.

6. The infection percentages in pine stands varied according to the degree of pine stocking, being highest in understocked stands.

7. The infection percentages in pine stands varied according to crown classes, being highest among dominant trees.

8. Destruction of all Ribes prevented the occurrence of new pine infections and permitted the area to be naturally restocked with disease-free seedlings.

INDEX

Page

Abortion—
bovine, infections, immunology, studies. By J. M. Buck and G. T. Creech 607-642
infections—
infection through injection of infected material 620, 621
of cattle, immunology, studies and experiments 607-642
Acala cotton—
growing and characters, comparisons .. 938-952, 954
spacing experiments in Southern California 1081-1093
Acid, production by *Bacillus larvae* 153-155
Acromania, cotton disease 803-828
Aecidiospores—
expulsion by the mayapple rust 923-926
uninucleated, in *Cacoma nitens* 1045-1058
Agglutination, tests for infectious abortion in cattle 613-614, 617-620
Alabama, climate, comparison with Japan .. 244-253
Alaska spring wheat, crosses with *vulgare* species, studies of results 1018-1031
Aldous, A. E., and Shantz, H. L.: Types of Vegetation in the Semiarid Portion of the United States 99-128
Alfalfa, wild, indicator of land value 101, 103, 117, 119
Alfieria, susceptibility to curly-top 314
Alimentary canal, bee larva 1184-1188, 1206
Alkali salts, Tempe, Ariz., chemical analyses 726
Alkaloids, insecticidal value 400
Allen, Ruth F., and Mackie, William W.: The Resistance of Oat Varieties to Stem Rust 705-720
Allison, F. E.—
Chemical and Biological Studies with Cyanamid and Some of Its Transformation Products 37-69
Greenhouse Experiments with Atmospheric Nitrogen Fertilizers and Related Compounds 971-976
The Effect of Cyanamid and Related Compounds on the Number of Microorganisms 1159-1160
The Nitrification of Phosphorus Nitride .. 1117-1118
Alsberg, Carl L., and Schwartze, Erich W.:
Pharmacology of Gossypol 191-197
Relation Between Toxicity of Cottonseed and its Gossypol Content 173-189
Amby wheat, crosses with emmer species, studies 1019-1031
Ammonia—
determination in nitrogenous materials .. 527-539
nitrogen, determination method 41-42
Ammonium sulphate—
effect on numbers of bacteria in soil 1160, 1161
nitrification rates, comparisons 43, 54-56, 58-60, 65
Analysis—
methods for meats 339-341
rye culms, normal and brittle 170
Anatomy, apple maggot 1-36
Anchusa spp., hosts of *Puccinia dispersa*, and infection methods 1119-1124
Ancylostoma caninum, occurrence in foxes 331
Anderson, M. S.: The Heat of Wetting of Soil Colloids 927-935
Angoumois grain moth, wheat infestation ... 1107, 1108, 1115
Animals—
immunization experiments for bovine abortion, detailed records 621-642
meat, edible viscera 339-346
undergoing gossypol poisoning, metabolism 192-194
Antelope brush, indicator of land value 109, 118, 122-126
Anthelmintic experiments with foxes 331-337

Page

Anthelmintics, literature 337
Antimony, insecticidal value 395, 396
Apelenchus ritzemabosi, description and occurrence on chrysanthemums 1061-1062
Apple—
blackrot—
fungus 583-488
review of work 589-590
maggot, anatomy and metamorphosis 1-36
peels, quercetin isolation and identification 1243-1245
Arizona—
cottons—
comparison 938-954
leaf-tissue fluids, chlorid content determination 695-704
Gila Valley, physiography, soils, and vegetation 724-725, 728-730
Arkansas, strawberry leather rot 368-371
Arlington Experiment Farm, wheat-rye hybrids 567-568, 573-575
Arrowweed, association with saltbush in Southwestern desert soils 770-772, 795-799, 800
Ascarids, control in foxes 334-337
Ascaris—
horse, toxicity 577-582
lumbricoides, toxicity 577-582
sensitization 577-582
Ascaron, active principle of Ascaris 579
Ascigerous stage of *Fusarium moniliforme*, and synonomy 909-922
Ash—
constituents in meats 340
lumber, steaming for control of powder-post beetle 1033-1038
Aspen, indicator of land value 116, 118, 123-125
Atriplex—
fasciculata, on southwestern desert soils 778
lentiformis, indicator of land value 113, 122
Avena spp., inoculation with stem rust, tests of resistance 706-709
Bacilli, causes of foulbrood 129-168
Bacillus—
alvei, discovery and relation to foulbrood. 131-133
aromatic, new species from dairy wastes. 275-276
brandenburgiensis, same as *Bacillus larvae*. 132, 133
larvae—
biochemical reactions, supplemental studies 150-157
growth in cultures, relation to sugar concentration 135-141
Back, E. A., and Cotton R. T.—
Effect of Fumigation Upon Heating of Grain Caused by Insects 1102-1116
Effective Use of Hydrocyanic-acid Gas in the Protection of Chick-peas Warehoused in 240-Pound Sacks 649-660
Relative Resistance of the Rice Weevil and the Granary Weevil to High and Low Temperatures 1043-1044
Bacteria—
cottonseed samples, effect on germination. 286
soil, numbers, effect of cyanamid and related compounds 1159-1166
Bacterial leafspot of Delphinium 261-270
Bacterium—
abortus cultures, use as vaccine to prevent abortion 609-620
delphinii, morphology, cultural characters, and description 264-269
flaccumfaciens, cause of bean wilt 490
phaseoli, cause of bean blight 490
sanguinarium, morphology 75-76
translucens, cause of bacterial blight of rye. 1039
Barberry, infection with *Puccinia graminis poae*, and spread of rust 541-542, 547
Barium—
carbonate, insecticidal value 396, 396
oxalate, insectidal value 396-396

Page

Barley, leaf rust, *Puccinia anomala*, aecial stages ... 1119-1126
Baston, G. H.: Studies of Wheat in Storage, and Heat Caused by Insects ... 1103-1104
Bean—
  disease, seed-borne, effect of moisture ... 489-497
  foliage burning, insecticides testing ... 402
  weevil, four-spotted, control, in chick-peas by hydrocyanic-acid gas ... 649-660
  weevils, fumigation ... 347-356
Beans—
  fertilizer experiments ... 972-974
  heating by insects, notes ... 1105, 1114
  navy, growing and yields, in seed-soaking experiments ... 490-496
Bee—
  diseases, literature cited ... 165-168
  larva, morphology ... 1167-1208
  larvae, effects of bacterial metabolism 163-164, 165
Bees—
  brood—
    diseases, relation to life history of bee larvae ... 130-135, 159-164
    food, composition ... 141-142
  foulbrood, causes and development ... 130-135
  larvae—
    composition at different ages ... 142-144
    feeding, cocoon-spinning, and quiescent stages ... 159-163
    life history relation to brood diseases ... 130-135, 159-164
    race, sex, and age, relation to foulbrood ... 130-132
Beetle—
  lady, squash, insecticides ... 401
  powder post, temperatures fatal, determination ... 1033-1038
Beetles, Japanese, insecticides ... 396-402
Beets—
  age of plants, relation to curly-top susceptibility ... 313-314
  growth and weight, effect of curly-top ... 303-304
  inoculation to produce curly-top ... 304-306
  losses from curly-top in California, 1917-1920 ... 301
  planting early to avoid leafhoppers ... 316
  resistant strains to curly-top disease ... 317
  sugar, curly-top disease, studies ... 297-320
Bibliography—
  bee diseases ... 165-168
  cereal rusts ... 718-719
  corn ear molds ... 921-922
  cotton growth diseases ... 897
  curly-top of beets ... 318-319
  cyanamid ... 68-69
  honeybee larva ... 1208-1212
  insect anatomy and metamorphosis ... 33-36
  plant growth factors ... 900-907
  sex studies of fowls ... 221-224
  sweet corn ... 440-443
Biguanid—
  nitrate, effect on numbers of bacteria in soil ... 1165, 1166
  nitrification in soils ... 40, 65
Binding power, soil colloids, factors influencing ... 499-513
Black spot, delphinium. *See* Leafspot, bacterial, of Delphinium.
Blackberry, orange rust, uninucleated aecidiospores ... 1045-1058
Blackrot, apple—
  fungus, comparison with fungus of currant cane blight ... 596-597
  fungus on apple and currant ... 583-588
  review of work ... 589-590
Blemishes, orange, relation to quality ... 521
Blight—
  bacterial, of rye ... 1039-1040
  bean, cause and comparison with wilt ... 490
Blister rust infection, survey, on pines at Kittery Point, Me. ... 1253-1258
Blossoming, effect of varying length of day ... 447-453
Blue mold rot, citrus fruits, prevention, borax treatment ... 961-968
Bolls, cotton—
  dwarfing, effects of crazy-top and other diseases ... 818-819
  shedding and development, comparisons ... 943-952

Page

Bones, skull, meadow mouse, description and variation ... 1001-1009, 1014
Borax, use in treatment of citrus fruits for the prevention of blue mold rot ... 961-968
Bordeaux spray, use against pecan scab ... 326-327, 329
Botryosphaeria ribis—
  association with *Physalospora malorum* on currant ... 584
  chromogena on apple and currant ... 594-596
  comparison with *Physalospora malorum* ... 596-597
  life history ... 590
  on currant and apple ... 589-598
Botrytis brown rot of strawberries, cause and description ... 646, 647, 648
Bots, ox, observations ... 271-274
Bowman, John J., and Fulton, Harry R.: Preliminary Results with the Borax Treatment of Citrus Fruits for the Prevention of Blue Mold Rot ... 961-968
Brachysm, cotton growth disorder ... 806-807
Braham, J. M.: Chemical and Biological Studies with Cyanamid and Some of its Transformation Products ... 37-69
Brain, bee larva, description ... 1172-1176, 1205
Brains, composition ... 344
Bran, heating by *Silvanus cassiae* ... 1105
Branching, abnormal, of cotton, effects of crazy-top and other diseases ... 813-814
Braun, Harry: A Gradient of Permeability to Iodin in Wheat Seed Coats ... 225-226
Breeding—
  chicken experimental study of sex ratio ... 200-220
  corn for improvement ... 435-436
Brewbaker, H. E.: Brittle Straw and Other Abnormalities in Rye ... 169-172
Briquettes, colloids, making, drying, and testing ... 501-511
Brittle straw, rye, and other abnormalities ... 169-172
Brood diseases, bee, relation to life history of bee larvae ... 130-135, 159-164
Brooks, Fred E., and Cotton, R. T.: The Cambium Curculio *Conotrachelus anaglypticus* ... 377-386
Brotherton, Wilber, Jr.: Gamete Production in Certain Crosses with "Rogues" in Peas ... 1247-1252
Brown rot of fruits in America, fungus causing ... 955-960
Bruchids, control in chick-peas by fumigation ... 649-660
Bruchus—
  obtectus, fumigation methods and results. 347-356
  quadrimaculatus—
    control in chick-peas by hydrocyanic-acid gas ... 649-660
    fumigation, methods and results ... 347-356
    See Bean weevil, four-spotted.
Bruchus spp., heat of grain, notes ... 1105, 1106, 1109-1112, 1114-1115
Brush varieties, indicator of land value ... 101, 108, 109, 114, 115, 117-127
Bryan, Mary K.: Bacterial Leafspot of Delphinium ... 261-270
Buck, J. M., and Creech, G. T.: Studies Relating to the Immunology of Bovine Infectious Abortion ... 607-642
Buckwheat, shrub, indicator of land value 112, 118, 121
Bud—
  abortion in Pima cotton, non-inheritance ... 2041-1042
  selection, relation to quality of crop in the Washington navel orange ... 521-526
  variations, citrus, progeny tests and performance records ... 522-525
Buds, citrus, progeny propagation and performance records ... 523-525
Buffalo grass, indicator or land value ... 102, 103, 117-121, 124
Bulb rot, Fusarium, of onion and relation to environment ... 683-694
Cabbage—
  clubroot infection, relation to temperature and moisture ... 553-557
  "hilling up" to control clubroot ... 557-558
Cacti, indicators of land value ... 112, 118, 121, 122, 127

Cucoma nitens— Page
occurrence without spermogonia..... 1047-1048
uninucleated aecidiospores and associated phenomena..... 1045-1058
See also Rust, orange.
Calandrinia menziesii, susceptibility to curly-top..... 314
Calcium—
compounds, effect on numbers of bacteria in soil..... 1163, 1164-1165
effect on orange-tree growth and composition..... 278, 281, 283
nitrate, effect on wheat growth..... 387-393
oxid, effect on numbers of bacteria in soil.. 1163, 1164-1165
California—
beet—
disease. *See* curly-top.
leafhopper and curly-top disease..... 279-320
climate, comparison with Alabama and Japan..... 249-252
Coachella Valley, physiography, soils, and vegetation..... 723, 725-727, 763
Southern, Acala cotton, spacing..... 1081-1093
Calliphora larva embryology, notes..... 6, 7, 8, 10, 20
Cambium curculio, *Conotrachelus anaglypticus*..... 377-386
Campbell, F. L., and Moore, William: Studies on Nonarsenical Stomach-Poison Insecticides..... 395-402
Cane—
blight fungus of currant, comparison with blackrot of apple..... 596-597
sugar, root disease, relation to snails..... 969-970
Cane-blight fungus of currant, on currant and apple..... 584, 589-598
Canker, citrus, susceptibility of citrus species, hybrids, and relatives..... 227-239
Canning, sweet corn, relative merits of varieties, etc..... 403-443
Carbon—
disulphid, use in control of bean weevils. 347-355
tetrachlorid, anthelmintic efficiency in treatment of foxes..... 331-337
Carpellate hemp plant, description..... 1068
Carsner, Eubanks, and Stahl, C. F.: Studies on Curly-top Disease of the Sugar Beet.. 297-320
Caryl, R. E.: Bud Selection as Related to Quality of Crop in the Washington Navel Orange..... 521-526
Casimiroa edulis, susceptibility to citrus canker..... 227
Castle, W. E., formula for estimating genetic factors..... 1098
Caterpillar, tent, insecticides testing..... 395-402
Cats, feeding with gossypol..... 191-196
Cats-claw, indicator of land value..... 112, 122
Cattle—
testing for abortion infection.... 613-614, 617-620
vaccination, control of infectious abortion 609-620
Ceanothus cuneatus, indicator of land value..... 116, 118, 120, 123, 126
Cecil clay loam subsoil, colloids from, breaking strength..... 511, 512
Cedar, reproduction after logging.... 1152-1154, 1157
Cells—
excretory, bee larva..... 1202
sap density, relation to environmental conditions in the Wasatch Mountains, Utah 845-907
Cereal rusts, physiological races, investigations and discoveries..... 705
Chaetospermum glutinosum, susceptibility to citrus canker..... 228
Chamiso, indicator of land value..... 101, 113, 116, 118, 121, 122, 125
Chaparral, indicator of land value..... 115, 119, 120, 125, 126
Chemicals, use on citrus fruits to prevent rot..... 961-963
Chenopodium spp., susceptibility to curly-top..... 314-315
Chickens—
breeding, experimental study of sex ratio. 200-220
flesh, vitamin B content, studies and experiments..... 463, 466-467, 468-469, 472
infection with fowl typhoid, studies and post-mortem findings..... 76-77
Chickens—Continued. Page
sex ratio—
experimental study and discussion..... 200-220
relation to antecedent egg production.. 199-234
Chick-peas—
heating caused by insect infestation..... 1106, 1109-1112, 1113, 1115
protection by hydrocyanic-acid gas fumigation..... 649-660
See also Peas, chick.
Chlorid, content of leaf-tissue fluids of cottons, Egyptian and Upland..... 695-704
Chlorophyll deficiency in rye..... 169
Chromosomes—
literature citations..... 680-681
maize and maize relatives..... 673-682
number in wheat, relation to morphological characters of hybrids..... 1028-1029
Chrysanthemum nema, *Apelenchus ritzema-bosi*, description..... 1061-1062
Ciboria fructicola, same as *Sclerotinia*..... 956, 957
Cicer arietinum. *See* Chick-peas; Peas, chick.
Citrus—
bud variations, progeny tests and performance records..... 522-525
fruits, blue mold rot prevention, results of borax treatment..... 961-968
growth in spring, required temperatures and relation to scab..... 243-253
hybrids, susceptibility to citrus canker 230-231, 235-239
plants, scab infection, conditions essential 243-253
scab—
cause, history, and distribution..... 241-242
relation to environmental factors..... 241-254
yearly prevalence, conditions determining..... 249-250
susceptibility to citrus canker..... 227-239
wild relatives, susceptibility to citrus canker..... 227-229, 232
Cladosporium citri, cause of citrus scab, environmental factors..... 241-254
Clarification methods in sugar determination, comparison..... 481-483
Clear-cut method of cutting Douglas fir, effect on reproduction..... 1233-1235, 1239-1241
Clearings, forest, effect on conditions of site 1149-1151
Club-leaf, cotton growth disorder..... 810
Clubroot—
effect of soil temperature and soil moisture 549-562
literature relating to..... 549-552, 559-561
Clustering, cotton growth disorder..... 806-807
Coachella Valley, California, cotton spacing.. 1081-1093
Coix lachryma jobi, pollen counts and chromosomes..... 677
Coleogyne, indicator of land value..... 110, 118, 121, 126, 127
Colloids—
literature cited..... 513
soil—
binding power, determination..... 506-508
binding power, factors influencing..... 499-513
binding power of different kinds..... 511
heat of wetting..... 927-935
Color—
picramate, dilution, effect..... 481
standards for sugar determination method.. 479-480, 486
Coloration, meadow mice..... 980-982, 1014
Colorimeter readings, values, factors for obtaining..... 483-484
Community plants for hot-water treatment of grain..... 79-80
Composite plants, subject to nematode galls. 474
Compounds, nitrogenous, effect on bacteria in soils..... 1159-1162
Conifer timber, indicator of land value..... 116, 120, 123-126
Conotrahelus—
anaglypticus—
distribution, description, life history, and control..... 377-386
See also Curculio, Cambium.
spp., literature concerning..... 386
Cook, O. F.: Acromania, or "Crazy-top," a Growth Disorder of Cotton..... 803-828
Copper, determination in meats..... 340

Page

Corethra larvae, notes 7, 10, 12
Corn—
  best canning stage 434
  canning—
    in quality tests, method 431
    literature, review and list 403–406, 440–443
    quality tests 431–433
  characters, correlation 1095–1102
  chromosome—
    number 673, 678–679
    number, comparison with related plants 673–682
  ear molds, literature citations 921–922
  ears, development in different varieties 412–414
  field, comparison with sweet corn in composition and canning value 425, 427, 428, 432, 435, 438
  hybrids, characters, inheritance and correlation 1097–1101
  injury by fungus *Fusarium moniliforme* 909, 910, 918
  kernel, toughness tests 414–422, 432, 438
  maturity, relation to quality of canned product 409–440
  silking period aid in determining maturity 409–411
  sugar content, relation to sweetness 434
  sweet—
    chemical studies, analysis methods, and discussion of results 418–431
    varieties for canning, relative merits, etc 403–443
    varieties, improvement by breeding 435–436
  varieties, analyses 424–425
  See also Maize.
Cornstarch juice, sugar determination, picric acid method 479–488

Cotton, R. T., and Back, E. A.:
  Effect of Fumigation Upon Heating of Grain Caused by Insects 1103–1116
  Effective Use of Hydrocyanic-acid Gas in the Protection of Chick-peas Warehoused in 240-Pound Sacks 649–660
  Relative Resistance of the Rice Weevil and the Granary Weevil to High and Low Temperatures 1043–1044

Cotton, R. T., and Brooks, Fred E.: The Cambium Curculio *Conotrachelus anaglypticus* 377–386

Cotton—
  abnormal branching, effects of crazy-top and other diseases 813–814
  Acala, spacing experiments in Southern California 1081–1093
  acromania or "crazy-top" 803–828
  bolls—
    injury by cambium curculio 379, 385
    shedding and development, comparison 943–954
  breeding and growth disorders 824
  Egyptian, chlorid content of leaf, comparison with Upland cotton 695–704
  fiber, salt content 293–295
  flowers and bolls, comparison of Pima with Upland 941–952
  growing on saline soils, relation to chlorid content 696, 701
  growth, irregularities caused by crazy-top and other diseases 813–819
  heredity, relation to growth disorders 822–823
  irrigated, spacing experiments in southern California, 1922 and 1923 1081–1093
  lint and seed characters, comparisons 950–952
  overwintering, study for disease spread 825
  Pima—
    comparison with Upland varieties in Arizona 938–954
    terminal bud abortion, noninheritance 1041–1042
  plants, dwarfing, effects of crazy-top and other diseases 813
  Upland—
    chlorid content of leaf, comparison with Egyptian cotton 695–704
    varieties, comparison with Pima cotton in Arizona 938–954
  varieties—
    susceptibility to crazy-top and other growth disorders 821–822
    variation of gossypol content in seed 177–178, 187

Page

Cotton—Continued.
  yield, comparison of Pima and Upland varieties 948–950
  yields in spacing experiments 1082–1093
Cottons, leaf tissue, chlorid content, comparison of Egyptian and Upland 695–704
Cottonseed—
  feeding tests, experiments with gossypol 173–198
  field germination, experiments 288–290
  germination 285–292
  gossypol content, variation with locality 173
  kernels, gossypol extraction and preparation 173–174
  laboratory germination, reports 290
  poisoning, feeding experiments 173–198
  "sensitive" samples, reasons for poor germination 286–291
  toxicity, relation to gossypol content 173–189
Couch, J. F.: Ascaris Sensitization 577–582
Coville, Frederick V.: Spiny-fruited Gooseberry from Florida 71–74
Cowpeas—
  heating by insects 1114
  silage, composition 258
  weevil infestation and fumigation 347–356
Cows, immunization experiments for bovine abortion, detailed records 633–635, 641–642
Craig, W. T., and Love, H. H.:
  The Genetic Relation Between *Triticum dicoccum dicoccoides* and a Similar Morphological Type Produced Synthetically 515–520
  The Inheritance of Pubescent Nodes in a Cross Between Two Varieties of Wheat 841–844
Cram, Eloise B.: A New Nematode, *Cylindropharynx ornata*, from the Zebra, with Keys to Related Nematode Parasites of the Equidae 661–672
Craterostomum spp., parasites of the Equidae 666, 668
Crazy-top, cotton—
  diagnosis 812
  disease 803–828
  irregular occurrence and different conditions of soil 819–821
  symptoms and effects, comparison with other disorders 813–819
Creatinin, determination method 340
Creech, G. T., and Buck, J. M.: Studies Relating to the Immunology of Bovine Infectious Abortion 607–642
Creosote bush, association on Southwestern desert soils 733–745, 795–799
Creosotebush, indicator of land value 111, 112, 118, 120–127
Crepis spp., seed infestation with nematodes 474, 475
Cross-breeding, wheat, for velvet nodes 841–844
Crucifers, clubroot disease, effect of soil temperature and soil moisture 549–562
Cryptolestes pusillus heating of grain 1105, 1115
Culpepper, C. W., and Magoon, C. A.: Studies Upon the Relative Merits of Sweet Corn Varieties for Canning, etc 403–443
Culture media for *Bacillus larvae*, and use 135–141
Cultures, *Bacterium abortus*, use as vaccine to immunize cattle 609–620
Curculio—
  cambium 377–386
  cambium, enemies and control methods 385, 386
Curly-leaf, beet. *See* Curly-top.
Curly-top—
  beet—
    distribution and the beet leafhopper 299–300
    economic importance 300–302
  causative organism 312
  disease—
    incubation period in insects and in plants. 306–307, 312
    sugar beets, studies 297–320
  effect on growth and weight of beets 303–304
  virus—
    overwintering 315
    transmission methods and factors affecting 306–316
Currant—
  cane blight fungus, on currant and apple 584, 589–598
  Physalospora malorum occurrence 583–588
Currants, black, spread of blister-rust infection 1253, 1255, 1257

Page

Cyanamid—
and dicyanodiamid nitrogen, determination method 42-43
bibliography 68-69
effect on microorganisms in soil 1159-1166
fertilizer tests 973-975
nitrification rates, comparisons 43-54
transformation products, changes in soil 54-66
Cyanids, insecticidal value 396-399
Cylicobrachytus spp., parasites of the Equidae 669
Cylicodontophorus spp., parasites of the Equidae 670
Cylicostephanus spp., parasites of the Equidae 671
Cylicostomum spp., parasites of the Equidae 666, 668, 670, 672
Cylicotoichus sp., parasite of the Equidae 669
Cylindropharynx spp., parasites of the Equidae 666, 668, 672
Cyliocercus spp., parasites of the Equidae 669
Cyclorrhapha, larvae 12, 14
Cytosis, cotton growth disorder 810
Dairy wastes, aromatic bacillus 275-276
Dandelion—
false, infestation with nematode of *Tylenchus dipsaci* 473-477
infestation with nematode, *Tylenchus dipsaci* 473, 475-477
Davison, F. R. and—
Brewbaker, H E., and Thompson, N. A.: Brittle Straw and Other Abnormalities in Rye 169-172
Willaman, J. J.: Some Modifications of the Picric Acid Method for Sugars 479-488
Day length—
effect on internodal length and leaf dimensions 453-460
relation to growth and sexual development of hemp 1069-1076
Daylight length, artificial control, effect on blossoming and growth 447-460
Dearstyne, R. S., and Kaupp, B. F.: Fowl Typhoid, Its Dissemination and Control 75-78
Delmas, pecan susceptibility to scab 322, 328
Delphinium, bacterial leafspot 261-270
Demaree, J. B.: Pecan Scab, with Special Reference to Sources of the Early Spring Infections 321-329
Denmark, clubroot studies in 550-552
Desert region, southwestern, natural vegetation, indicator significance 721-802
Desert-sage, association on Southwestern desert soils 745-757, 796-799
Dessication, effect on virus of curly-top 311
Devarda alloy, use in nitrate determination 527, 528-538
Diarrhea, caused by gossypol 192
Dicyanodiamid, nitrification in soils and effects on fertilizers 39-40, 54-61
Dimorphism, sexual, of hemp, factors affecting 1067-1078
Diplodia natalensis, growing on apple and currant twigs 587
Dipsacus fullonum, seed infestation with nematodes 474, 477
Diptera, anatomy, embryology, and metamorphosis 6, 7, 8, 12, 20, 28, 30, 31
Dodge, B. O.—
and Stevens, Neil E.: The Rhizoctonia Brown Rot and Other Fruit Rots of Strawberries 643-648
Expulsion of Aeciodiospores by the May-apple Rust, *Puccinia podophylli* 923-926
Uninucleated Aecidiospores in the *Caeoma nitens* and Associated Phenomena 1045-1058
Donkey, parasites 666-672
Dormant spray for pecan scab 327
Dorylaimus regius, description, habits, and food 1062-1064
Dothiorella pycnidia, from currant cane blight fungus, etc 590, 591
Drummond, Pearl L., and Toole, Eben S.: The Germination of Cottonseed 285-292
Dry farming land, indications of natural vegetation 117
Ducks, flesh, vitamin B content 463, 468, 472
Duff, moisture and temperature fluctuations, comparison with bare soil 1154-1156

Page

Dunegan, John C., and Roberts, John W.: The Fungus Causing the Common Brown Rot of Fruits in America 955-960
Durango cotton, growing and characters, comparisons 938-952, 954
Dusts, insoluble aromatic compounds, insecticidal value 401
Dycyanodiamide, fertilizer tests 973-975
Ear—
corn, development in different varieties 412-414
length, meadow mouse 988
Earths, alkaline determination in meats 341
Eberthella sanguinaria, same as *Bacterium sanguinarium* 75, 77
Edema, caused by gossypol poisoning 195
Eelworms. *See* Nematodes.
Egg production—
relation to the sex ratio of—
chickens 207-209
the domestic fowl 199-224
Eggs—
consumption, per capita 461
Vitamin content 461-472
weight, realtion to sex ratio of chickens 209-211
Egyptian cotton, chlorid content of leaf tissue, comparison with Upland 695-704
Embryos, meadow mouse, number and weight 989
Emmer, wheat group, characters 1017
Emmers—
comparison of synthetic form with wild form 515-520
wild, study and comparisons 515-520
Encelia farinosa, indicator of land value 112, 122
Endophyllum spp., characteristics 1050, 1052, 1053
Ensiling Sudan grass with a legume 255-259
Epiornithological studies of fowl typhoid 78
Equidae, nematode parasites 666-672
Eremocitrus glauca, susceptibility to citrus canker 226
Eristalis sp., larvae 8, 10, 13, 20
Erodium cicutarium. *See* Alfilaria.
Ether extract, determination in meats 340
Euchlaena spp., chromosome number, pollen counts, etc 673-676
Eutettix tenella. *See* Leafhopper, beet.
Fasciation, cotton, effects of crazy-top and other diseases 814
Fat—
cells, bee larva, description 1200-1201
tissue of apple maggot and other larvae 16-19
Feeding—
cottonseed, experiments with gossypol 173-198
pigeons, with poultry flesh and eggs 463-471
Ferona spp., susceptibility to citrus canker 228
Fertilizers—
nitrate determination methods 533-538
value of phosphorus nitride and ammonium sulphate, comparison 1118
Fescue, indicator of land value 107, 117, 122
Fiber, cotton, salt content 293-295
Fir, Douglas—
cutting methods, effect on reproduction 1233-1242
reproduction—
after logging 1152-1154, 1157
on pine lands of central Idaho 1140-1147
under various cutting methods 1233-1242
Fixed Nitrogen Research Laboratory, fertilizer experiments 971-976
Flats, bare, southwestern desert soils 779
Flavobacterium suaveolens, a new species of aromatic bacillus from dairy wastes 275-276
Florida, gooseberry, spiny-fruited, native species 71-74
Flowers, cotton, abnormalities, effects of crazy-top and other diseases 813
Fly, apple maggot—
anatomy and metamorphosis, notes, and bibliography 1-36
technical description 21-30, 32
Foot—
meadow mouse, hind, measurement 987
meadow mouse, plantar tubercles variation 983, 1014
Ford, E. R., and Posey, G. B., Survey of Blister Rust Infection on Pines at Kittery Point, Me., etc 1253-1258

Page

Forest—
distribution, relation to sap density..... 892-895
reproduction—
after logging in northern Idaho..... 1149-1157
injury by grazing and other causes... 1145-1146
Fortunella—
hindsii, susceptibility to citrus canker..... 228
spp., susceptibility to cirtus canker..... 228
Foulbrood—
causes and development..... 130-133
European, organisms associated with..... 129, 130, 132, 135
relation to the metabolism of its causative organism..... 129-168
Fowl—
domestic. *See* Chicken.
typhoid, dissemination and control..... 75-78
Fowls—
infected with typhoid, description, symptoms, and results..... 76, 77
vaccination for control of typhoid..... 78
Foxes, treatment with carbon tetrachlorid. 331-337
Frederich, William J., and Peltier, George L.:
Further Studies on the Relative Susceptibility to Citrus Canker of Different Species and Hybrid of the Genus Citrus, etc..... 227-239
Relation of Environmental Factors to Citrus Scab Caused by *Cladosporium citri* Massee..... 241-254
Freezing, soil, limiting factors in sap density of plants..... 894
Fruit, sound, immunity to cambium curculio..... 378, 379
Fruits, brown rot, fungus causing..... 955-960
Fulton, Harry R., and Bowman, John J.:
Preliminary Results with the Borax Treatment of Citrus Fruits for the Prevention of Blue Mold Rot..... 961-968
Fumigation—
effect upon heating of grain caused by insects..... 1103-1116
effects on bean weevils, adults, eggs, and forms within seeds..... 348-355
grain warehouses, experiments with chick peas..... 650-659
Fungi, sporocarps, relation of size and structure to host..... 586-587
Fungus—
brown rot, literature..... 959-960
causing brown rot of fruits in America... 955-960
Fusarium—
bulb rot of onion, and relation of environment to development..... 683-694
cepae—
cause of onion bulb rot, description, etc. 684-688
realtion to temperature, acidity, and alkalinity..... 685-686
moniliforme—
an ascigerous stage and synonomy..... 909-922
culture studies on conidia..... 910, 913-916
Fusicladium effusum, cause of pecan scab, nature and control..... 324-328
Gaines, E. F., and Sax, Karl: A Genetic and Cytological Study of Certain Hybrids of Wheat Species..... 1017-1032
Galleta, indicator of land value..... 106, 118, 119, 125
Galls, nematode, occurrence on composite plants..... 473-477
Gemete production in certain crosses with "rogues" in peas..... 1247-1252
Genetics, wheat, literature..... 1031-1032
Germination—
cottonseed..... 285-292
seed, western white pine, by seasons... 1127-1 28
western white pine, relation to surfaces. 1151-1154
wheat, effect of modified hot-water treatment..... 80-89
Gestation, meadow mouse, period and number of young..... 989
Gibberella—
acervalis, similarity to *Fusarium moniliforme*..... 917
moniliformis, technical description..... 920
saubinetii, similarity to *Fusarium moniliforme*..... 914
Glands, silk, bee larva..... 1189-1190, 1207
Glycogen, utilization in metabolism of *Bacillus larvae*..... 151-153

Page

Godfrey, G. H.: Dissemination of the Stem and Bulb Infesting Nematode *Tylenchus dipsaci*, in the Seeds of Certain Composites..... 473-478
Godkin, James, Johnson, A. G., and Reddy, C. S.: Bacterial Blight of Rye..... 1039-1040
Gonads, rudiments in bee larva..... 1202-1203
Gooseberries, eradication for blister rust unnecessary in Southeast..... 74
Gooseberry, spiny-fruited, from Florida..... 71-74
Gossypol—
content of cottonseed, relation to toxicity. 173-180
extraction from cottonseed and preparation..... 173-174
intraperitoneal injection into animals..... 174-178
literature concerning..... 188-189, 197
pharmacology..... 191-196
Gradus peas, rogue type, crossing and backcrossing..... 1247-1252
Grain—
fumigation, effect on heating caused by insect infestation..... 1103-1116
heating in storage, causes..... 1108-1114
insects, control in warehouses, experiments with chick-peas..... 649-660
land, indications of natural vegetation..... 117
pests, literature citations..... 1116
treatment with hot water, community plants..... 79-80
Grama grass, indicator of land value..... 100, 103, 104-105, 106, 117-122
Granary weevil, resistance to high and low temperatures..... 1043-1044
Grapefruit—
scab infection, temperature limits..... 243
treatment with borax to prevent rot..... 965, 968
Grasses—
indicators of land value... 101-107, 112-114, 117-127
inoculation with rust, *Puccinia graminis poae*..... 541-543
Grazing—
injury to conifer reproduction..... 1145, 1146
land, indications of natural vegetation..... 118
lands, carrying capacity of vegetation.... 119-121
Greasewood, indicator of land value..... 110, 118, 120, 125, 126
Greenhouse—
experiments with atmospheric nitrogen fertilizers and related compounds..... 971-976
onion rot, studies and experiments..... 687-688
Grossularia—
curvata, description, comparison with *G. echinella*..... 71-73
echinella, spiny-fruited gooseberry from Florida, description, etc..... 71-74
spp., American, comparison with *echinella*. 72-74
Guanidin—
nitrate, effect on numbers of bacteria in soil..... 1165, 1166
nitrification in soils..... 40, 63, 65-66
Guanylurea—
effect on numbers of bacteria in soil..... 1161, 1165, 1166
fertilizer tests..... 973-975
nitrification in soils and rate of decomposition..... 40, 56-58, 62, 64
Guinea—
fowl, flesh, vitamin B content..... 463, 468, 472
pigs, inoculation with milk from diseased cows..... 622-642
Gyalocephalus spp., parasites of Equidae.... 666, 667
Gymnoconia interstitialis, spore discharge from aecidia..... 925
Haas, A. R. C., and Reed, H. S.: Some Relations Between the Growth and Composition of Young Trees and the Concentration of the Nutrient Solution..... 277-284
"Hairy neck"—
character of rye, investigations..... 568-571
wheat segregates from wheat-rye hybrids. 567-576
Hanson, Karl B., and Van Volkenberg, H. L.:
Anthelmintic Efficiency of Carbon Tetrachlorid in the Treatment of Foxes..... 331-337
Hardiness, plant, relation to sap density... 898-899
Hare, European—
habits, control, and value for food and sport..... 1133-1137
in North America..... 1133-1137

Page

Hares, European, introduction, distribution, and abundance ... 1134-1136
Harris, J. Arthur: The Chlorid Content of the Leaf-Tissue Fluids of Egyptian and Upland Cotton ... 695-704
Harrison, W. T.: Ascaris Sensitization ... 577-582
Hartsville cotton, growing and characters, comparisons ... 938-952, 954
Head, meadow mouse—
and development of skull ... 989-992
measurement and body ... 985-987
Heart—
bee larva, and blood cells ... 1195-1200, 1207
enlargement, caused by gossypol ... 196
Hearts, composition ... 344
Heat—
effect on virus of curly-top ... 311
in stored grain, caused by insect infestation ... 1103-1114
wetting, of soil colloids ... 927-935
Heifers, immunization experiments for bovine abortion ... 621-633, 636-641
Hemlock, reproduction after logging ... 1152-1154, 1157
Hemp—
flower mutilation, effect on sex development ... 1077-1078
growth, relation to length of daylight ... 1070-1074
sex, influence of environment ... 1067-1080
Hens, flesh, vitamin B content ... 463, 466-467, 468-469, 472
Herbs, Wasatch Mountains, freezing point, depressions, and osmotic pressures ... 871-875, 880-884
Herds, bovine abortion, vaccine treatment ... 617-620
Hesperethusa crenulata, susceptibility to citrus canker ... 228
Hessian fly—
parasite *Platygaster vernalis*—
development and feeding ... 833-837
polyembryonic development ... 829-840
Hilaria rigida, indicator of land value ... 106, 118, 121
Hill, C. C., and Leiby, R. W.: The Polyembryonic Development of *Platygaster vernalis* ... 829-840
Hip glands, meadow mouse, variations ... 984-985, 1014
Hoagland, Ralph, and—
Lee, Alfred R.: Anfineuritic Vitamin in Poultry Flesh and Eggs ... 461-472
Powick, Wilmer C.: The Chemical Composition of Edible Viscera From Meat-producing Animals ... 339-346
Holding tests, citrus fruits treated with chemicals for prevention of rot ... 961-963
Honeybee—
cluster, heat production ... 1109
fat tissue in larvae and in mature insects ... 16, 17, 18, 19
larva, morphology ... 1167-1214
Hookworm, fox, treatment with carbon tetrachlorid ... 331-337
Hopperdozer, use in control of leafhopper ... 316
Horse—
Ascaris, fluid extract eye-test experiments on horses ... 577, 580, 581, 582
parasites ... 666-672
Hot-water treatment, injury to wheat, relation of seedcoat protection ... 86-89
Howell, A. Brazier: Individual and Age Variation in *Microtus montanus yosemite* ... 977-1016
Humus depth, relation to root length of forest seedlings ... 1238-1239
Hybosis, cotton growth disorder ... 809-810
Hybrid—
maize, Jala and Tom Thumb, character inheritance, etc ... 1097-1101
teosinte-and-corn, pollen counts and chromosomes ... 671-676
Hybrids—
citrus, susceptibility to citrus canker ... 230-231, 235-239
wheat species, study, genetic and cytological ... 1017-1032
wheat-rye, "hairy neck" segregates ... 567-576
Hydrocyanic-acid gas—
fumigation of grain for insect pests ... 1106, 1113, 1114, 1115

Page

Hydrocyanic-acid gas—Continued.
use in—
control of bean weevils ... 347-355
protection of chick-peas in 240-pound sacks ... 649-660
Hypochaeris radicata. *See* Dandelion, false.
Hypoderma—
bovis, second-stage larva, comparison with *H. lineatum* ... 274
lineatum, larval stages, comparison of characters ... 271-274
Idaho—
central, growth on cut-over and virgin western yellow pine lands ... 1139-1148
northern, reproduction after logging, some factors affecting ... 1149-1157
Priest River Forest Experiment Station, pine-seed sowing ... 1127-1131
Imaginal buds, apple-maggot larvae ... 7-8
Indiana, wheat treating in community plants ... 79-80
Inoculation—
oats with stem rust to test varietal resistance, results ... 710-718
onion with Fusarium bulb rot, greenhouse experiments ... 687-688
Insect galls in grain, notes ... 1109
Insecticides—
nonarsenical stomach-poison, studies ... 395-402
testing—
method ... 395
on insects and on bean foliage ... 395-402
Insects—
carriers of crazy-top disease, study ... 825
cause of heating in grain ... 1103-1114
forest, losses caused to pine and Douglas fir ... 1144
number, relation to curly-top and variation of individuals ... 307-310
Internodal length, effect of varying day length ... 453-460
Internodes, cotton, irregularity, effects of crazy-top and other diseases ... 815
Involucres, abnormal, of cotton, effects of crazy-top and other diseases ... 817
Iodin, permeability gradient in wheat seed coats ... 225-226
Iron determination in meats ... 341
Ironwood, indicator of land value and possibilities ... 112, 122
Jackson, H. S., and Mains, E. B.: Aecial Stages of the Leaf Rusts of Rye and of Barley in the United States ... 1119-1126
Jacob, K. D.: Chemical and Biological Studies with Cyanamid and Some of its Transformation Products ... 37-60
Jala maize, crossing with Tom Thumb maize, results ... 1095-1102
Japan, climate, comparison with Alabama and California ... 249-252
Job's tears, pollen counts and chromosome number ... 677
Johnson, A. G., Reddy, C. S., and Godkin, James: Bacterial Blight of Rye ... 1039-1040
Jull, M. A.: The Relation of Antecedent Egg Production to the Sex Ratio of the Domestic Fowl ... 199-224
Kaupp, B. F., and Dearstyne, R. S.: Fowl Typhoid, its Dissemination and Control ... 75-78
Kearney, Thomas H.—
Non-inheritance of Terminal Bud Abortion in Pima Cotton ... 1041-1042
The Salt Content of Cotton Fiber ... 293-295
Kempton, J. H.: Correlation Among Quantitative Characters in Maize ... 1095-1102
Kernel, corn, toughness tests ... 414-422, 432, 438
Kidneys, composition ... 344
Kigelia pinnata, host plant of *Heterodera radicicola* ... 1061
King, C. J.: Comparison of Pima Cotton with Upland Varieties in Arizona ... 937-954
Korstain, C. F.—
Density of Cell Sap in Relation to Environmental Conditions in the Wasatch Mountains of Utah ... 845-907
Growth on Cut-over and Virgin Western Yellow Pine Lands in Central Idaho ... 1139-1147

Page

Kubanka—
durum wheat, crosses with black winter emmer ... 516–519
wheat, crosses with *vulgare* species ... 1019–1031
Kumquats, resistance to citrus canker ... 228
Laake, E. W.: Further Observations on the Molts of the Ox Bots, *Hypoderma bovis* De Geer and *H. Lineatum* Villiers ... 271–274
Land, agricultural potentiality characterized by plant associations ... 800–801
Larch, reproduction after logging ... 1152–1154, 1157
Larkspur—
disease, bacterial leaf spot, cause and control ... 261–270
inoculation with leafspot bacteria ... 263–264
Larsen, J. A.: Some Factors Affecting Reproduction After Logging in Northern Idaho ... 1149–1157
Larson, A. O.: Fumigation of Bean Weevils *Bruchus obtectus* and *B. quadrimaculatus* ... 347–356
Larva, bee, description, anatomy, and histology of various parts ... 1167–1208
Larvae—
apple maggot, development ... 1–21
bee, composition at different ages ... 142–150
Lasioderma serricorne, control in chick-peas ... 649, 658
Lawrence—
John V.: The Chlorid Content of the Leaf Tissue Fluids of Egyptian and Upland Cotton ... 695–704
Zonja Wallen: The Chlorid Content of the Leaf Tissue Fluids of Egyptian and Upland Cotton ... 695–704
Lead arsenate, insecticidal value, comparison with cuprous cyanid ... 399
Leaf—
dimensions, relation to varying day length ... 453–460
forms, cotton, abnormal, effects of crazy-top and other diseases ... 815–816
orange, sap concentration and reaction, relative constancy ... 277
Leaf-curl, cotton, growth disorder ... 809–810
Leaf-cut, cotton growth disorder ... 807–809
Leafhopper—
beet—
control method ... 316–317
distribution ... 299–300
transmission of curly-top disease ... 306–310
curly-top virus incubation period ... 306–308
Leafspot, bacterial, of Delphinium ... 261–270
Leather rot—
of strawberries, cause and description ... 646–648
strawberry ... 357–376
Leaves—
conifer, sap density seasonal variations ... 889–892
cotton, discoloration, effect of mosaic diseases ... 816–817
pecan, scab description and source of infection ... 322–323, 325
young orange trees, composition ... 282, 283
Lee, Alfred R., and Hoagland, Ralph: Antineuritic Vitamin in Poultry Flesh and Eggs ... 461–472
Legumes, sowing with Sudan grass for silage mixture ... 256–257
Leiby, R. W., and Hill, C. C.: The Polyembryonic Development of *Platygaster ternalis* ... 829–840
Leighty, Clyde E., and Taylor, J. W.: Hairy Neck Wheat Segregates from Wheat-Rye Hybrids ... 567–576
Lemons, treatment with borax to prevent rot, experiments ... 962–968
Leonard, Lewis T.: Effect of Moisture on Seed-borne Bean Disease ... 489–497
Lepus europaeus, in North America ... 1133–1137
Levine, M. N., and Stakman, E. C.: *Puccinia graminis poae* Erikss. and Henn. in the United States ... 541–548
Light, relation to curly-top infection ... 310
Limbs, variations, progeny tests ... 522–523
Lime content of cyanamid, relation to increase of soil bacterial numbers ... 1163–1164
Lime-sulphur wash, as repellant on orchard trees ... 1137
Liming soil, effect on clubroot ... 551, 558
Lint cotton, comparisons ... 950–952

Page

Livers—
antineuritic value ... 469, 472
composition, table ... 342–343
Logging, effect on forest cover and reproduction ... 1149–1157
Lone Star cotton, growing and characters, comparisons ... 938–952
Longley, Albert E.: Chromosomes in Maize and Maize Relatives ... 673–682
Loomis, H. F.: Comparison of Pima Cotton with Upland Varieties in Arizona ... 937–954
Louisiana, sugar-cane root disease, relation to snails ... 969–970
Love, H. H., and Craig, W. T.:
The Genetic Relation Between *Triticum dicoccum dicoccoides* and a Similar Morphological Type Produced Synthetically ... 515, 520
The Inheritance of Pubescent Nodes in a Cross Between Two Varieties of Wheat ... 841–844
Lyctus planicollis. *See* Beetle, powder-post; Powder-post beetle.
Mackie, William W., and Allen, Ruth F.: The Resistance of Oat Varieties to Stem Rust ... 705–720
Maggot, apple anatomy and metamorphosis ... 1–36
Magnesium sulphate, effect on wheat growth ... 387–393
Magnesium-oxid method of nitrate determination, comparisons ... 536–538
Magoon, C. A., and Culpepper, C. W.: Studies Upon the Relative Merits of Sweet Corn Varieties for Canning, etc ... 403–443
Mahogany, mountain, indicator of land value and possibilities ... 115, 118, 120, 123, 124, 125
Maine—
Experiment Station, wheat hybrids, growing experiments ... 1019
Kittery Point, pines' infection with blister rust, etc., survey ... 1253–1258
Mains, E. B., and Jackson, H. S.: Aecial Stages of the Leaf Rust of Rye and of Barley in the United States ... 1119–1126
Maize—
characters, correlation ... 1095–1102
See also Corn.
Malpighian tubules, bee larva ... 1188–1179, 1207
Malva parviflora, susceptibility to curly-top ... 315
Mammals, small, preparation of skulls for collection ... 978–979
Mammae, meadow mice ... 983, 1014
Mandible, meadow mouse, description and variation ... 1009, 1015
Map, western United States, key to vegetation regions ... 100, 123–127
Marquis wheat crosses with emmer species ... 1019–1031
Matchweed, indicator of land value and possibilities ... 101, 103, 104, 119–125
Maturity, corn, tests for canning stage ... 434
Mayapple rust, expulsion of aecidiospores ... 923–926
McClelland, T. B.: The photoperiodism of *Tephrosia candida* ... 445–460
McKeever, H. G.: Spacing Experiments with Acala Cotton in Southern California ... 1061–1093
McPhee, Hugh C.: The Influence of Environment on Sex in Hemp, *Cannabis sativa* ... 1067–1080
Meadows, vegetation type, indicator of land value ... 108
Meat, hare, food value and quantity, estimate ... 1137
Mebane cotton, growing and characters, comparison ... 938–952
Melophagus ovinus, embryology studies ... 6, 10–11, 13
Mesquite—
association with chamiso on southwestern desert soils ... 766–769, 796–799, 800
indicator of land value and possibilities ... 103, 112, 113
thicket on southwestern desert soils ... 757–759
Metals, alkali, determination in meats ... 341
Mice, meadow—
characters, variations with sex and age ... 977–1016
male and female, measurement ... 981–982, 1014
measurement, methods employed and results ... 979, 985–988, 1014
Microcitrus, susceptibility to citrus canker ... 228, 230
Microorganisms in soil, effect of cyanamid and related compounds ... 1159–1166

Microtus montanus yosemite— Page
variation, individual and age 977-1016
See also Mouse, meadow; Mice, meadow.
Middleton, Howard E.: Factors Influencing the Binding Power of Soil Colloids 499-513
Milk, infection with abortion bacteri 614, 620
Minnesota rye, abnormalities occurrence 169
Mistletoe, losses caused to Douglas fir in Idaho forests 1144-1145
Mixtures, silage crops, typical combinations 255
Moisture—
content, sweet corn 426
cottonseed, relation to germination 290-291
determination in meats, method 339
effect on—
forest reproduction 1235-1236
seed-borne bean disease 489-497
relation to citrus scab infection and development 243-253
Molds, corn ear, studies 909-922
Molting, meadow mice 983, 1014
Molts, ox bots, observations 271-274
Montana, Lola National Forest, Savanac nursery pine-seed sowing 1127-1131
Monteith, John, Jr., Relation of Soil Temperature and Soil Moisture to Infection by *Plasmodiophora brassicae* 549-562
Moore, William, and Campbell, F. L.: Studies on Nonarsenical Stomach-poison Insecticides 395-402
Morphology, honeybee larva 1167-1214
Mortality, prenatal, in chickens, relation to sex ratio 202-207
Mountain weed, indicator of land value and possibilities 108, 118, 122-126
Mouse, meadow—
coloration and other characters, variations 980-1014
skull, description, and measurement of bones and teeth 993-1014
variation, individual and age 977-1016
Mulching strawberries for prevention of rot 374
Mules, parasites, key 666-672
Mummy peas, crossing with Gradus rogue and Rice's 330 1247-1248
Muscles, bee larva, head and trunk, description 1190-1195, 1207
Muscoidae, anatomy, embryology, and metamorphosis 8, 10, 14-15, 29, 30
Myiophasia globosa, enemy of cambium curculio 385, 386
Needlegrass, indicator of land value and possibilities 102-105, 117, 120, 121, 1214
Nelson, James A.: Morphology of the Honeybee Larva 1167-1214
Nemas, parasitic, on plants and related forms 1059-1066
Nematode—
Cylindropharynx ornata, from the zebra, with keys to other nematode parasites 661-672
new, *Cylindropharynx ornata*, of zebra 661-672
Tylenchus dipsaci, dissemination in seeds of certain composites 473-478
Nematodes—
literature relating to 478
plant, literature citations 1065-1066
Nervous systems, bee larva, brain, ventral nerve cord, etc 1172-1179, 1205
Netting, poultry, use in protecting trees against hares 1137
Niggerwool, indicator of land value and possibilities 100, 101, 102, 104, 118, 120-125
Nitrate—
determination in—
fertilizers, comparison of methods 533-536
nitrogenous materials 527-539
formation from cyanamid and urea in soils 49-53
nitrogen determination method 42-43
Nitrification of phosphorus nitride 1117-1118
Nitrogen—
atmospheric, fertilizers, greenhouse experiments 971-976
determination in meats 340
importance in wheat growth and development 393
Nitrogenous— Page
compounds, analysis, methods 41-43
materials, nitrate and ammonia determination 527-539
Nodes, pubescent, inheritance in a cross between two varieties of wheat 841-844
Nolina, indicator of land value and possibilities 114, 118, 120, 123
Nonarsenical stomach-poison insecticides 395-402
Northoscordium bivalve, host of *Uromyces hordei* 1124
Nut, pecan, scab, description and source of infection 323, 325
Nutrient solution—
concentration, relation to orange trees, growth and composition 277-284
molecular proportions, relation to wheat growth 387-393
Shive's formula 388
Oak, lumber, steaming for control of powder-post beetle 1033-1038
Oats—
breeding, for resistance to stem rust, and results 706
inoculation with stem rust, tests of resistance in varieties 706-709
resistant to stem rust, list of varieties 706
stem rust, resistance by oat varieties 705-720
varieties—
inoculation with stem rust to test resistance, results 710-718
resistance to stem rust 705-720
Ocotillo, indicator of land value and possibilities 112, 118, 122, 127
Oenocytes, bee larva, description 1201-1202
Oesophagodontus spp., parasites of Equidae, key 666, 667
Onion—
diseases, literature citations 693-694
Fusarium bulb rot, and relation of environment to development 683-694
seedlings, infestation with nematodes 477
storage, relation of temperature to rot development 691-692, 693
Onions, inoculation with Fusarium bulb rot, greenhouse experiments 687-688
Oospora verticilloides, similarity to *Fusarium moniliforme* 918-920
Orange—
Thompson strain, progeny propagation of limb variations, results 522-525
trees, growth and composition, relation to nutrient solution 277-284
Valencia, effect of concentration of solution on young trees 280-281
Washington navel, quality of crop as related to bud selection 521-526
Oranges—
brown-spotted, from limb variations 522
factors determining quality of crop 521
leaf sap, concentration and reaction, relative constancy 277
rind, juice, color, size, and shape, relation to quality 521
scab infection, temperature limits 243
treatment with borax to prevent rot, experiments 961-968
Ornithogalum spp., host of *Puccinia anomola*, aecial stage 1124-1125
Orthorrhapha larvae, notes 12, 14
Osmotic phenomena, relation to cell sap concentration 846-847
Ovaries, honeybee queen larva 1203
Ox bots, molts, observations 271-274
Palms, growing in desert soils, Coachella Valley 763-764
Paloverde, indicator of land value and possibilities 112, 122
Paralysis, caused by gossypol poisoning 194
Paramignya monophylla, susceptibility to citrus canker 228
Parasite, Hessian fly, *Platygaster vernalis*, polyembryonic development 829-840
Parasites—
nematode—
literature citations 672
of the Equidae, horse, donkey, mule, and zebra, key 666-672

Page

Paratylenchus nanus infestation of zinnia roots ... 1064-1065
Parosela arborescens, indicator of land value and possibilities ... 113, 122
Pasture, gains of steers, effects of winter rations ... 1215-1232
Patellina fragaria, cause of tan rot of strawberries ... 645
Peas—
crossing, gamete production ... 1247-1252
mutations in cross breeding ... 1247-1252
Pecan—
scab, and sources of early spring infections 321-330
trees, spraying, difficulties ... 328
Pecans—
growing in Southeast, and distribution of scab ... 321
spraying for scab-control experiments ... 326-327
varietal susceptibility to scab ... 322, 325
Peels, apple, quercetin isolation and identification ... 1243-1245
Pellagra, relation to *Cospora vertucilloides* on corn, discussion ... 918
Peltier, George L., and Frederich, William J.: Further Studies on the Relative Susceptibility to Citrus Canker of Different Species and Hybrids of the Genus Citrus, etc ... 227-239
Relation of Environmental Factors to Citrus Scab Caused by *Cladosporium citri* Massee ... 241-254
Pests, grain, literature citations ... 1116
Pezizella lythri, cause of tan brown rot of strawberries ... 647, 648
Pharmacology, gossypol ... 191-196
Pharynx, apple maggot larvae ... 8-15
Phenol, effect on nitrification of cyanamid ... 53-54
Phlox, *Cephalobus* occurrence ... 1059-1061
Phosphorus—
determination in meats ... 340
nitride, nitrification, comparison with ammonium sulphate ... 1117-1118
Photoperiodism of *Teprosia candida* ... 445-460
Physalospora malorum—
comparison with *Botryosphaeria ribis* ... 596-597
on currant ... 583-588
spores from apple and currant, comparison 585-586
Phytophthora cactorum, cause of leather rot of strawberries ... 357, 358-366, 646, 647, 648
Pickleweed—
association on Southwestern desert soils ... 764-766, 796-797, 800
indicator of land value and possibilities ... 111, 118, 121, 122, 126, 127
Picric acid—
effect on glucose and fructose ... 480-481
method of sugar determination, modifications ... 479-488
purifying for sugar tests ... 485-486
Piemeisel, R. L., and Shantz, H. L.: Indicator Significance of the Natural Vegetation of the Southwestern Desert Region ... 721-802
Pigeons, feeding with poultry flesh and eggs, experiments ... 462-471
Pima cotton—
comparison with Upland varieties in Arizona ... 938-954
fiber, salt content ... 293-295
Pine—
lands, central Idaho, growth and reproduction of pine and Douglas fir ... 1139-1147
lumber, growth in Douglas fir stands ... 1237, 1239, 1240
reproduction after logging ... 1152-1154, 1157
western—
white, germination, relation to surfaces ... 1151-1154
white, seed, fall sowing and delayed germination ... 1127-1131
yellow, growth on cut-over and virgin lands in central Idaho ... 1139-1148
yellow, losses in central Idaho, causes ... 1143-1145
Pines—
blister rust infection at Kittery Point, Me., and effect of *Ribes* eradication ... 1253-1258
hard, immunity to blister rust ... 74
infection by blister rust, relation to size and density of stand ... 1255-1257

Page

Plant—
communities on desert soils, detailed description ... 730-779
growth, effect of varying the day length ... 451-453
succession, relation to sap density ... 892-895
Plants—
desert—
associated on southwestern desert region, description ... 730-779
list, with botanical names ... 781
dioecious, sex reversal, discussion ... 1079
food supply, seasonal variations ... 891-892
growth and reproduction, relation to sap density ... 895-896
semiarid, indicators of land values ... 100-127
structure and physiology, variation with environment ... 896-898
susceptibility to curly-top disease ... 314-315
Plasmodiophora brassicae, infection, relation of soil temperature and soil moisture ... 549-562
Platygaster vernalis—
egg description and development ... 830-833
life history and embryonic development ... 829-838
polyembryonic development ... 829-840
Plodia interpunctella, control in warehouses by fumigation ... 649, 659
Pluchea sericea, indicator of land value ... 113, 122, 127
Poa spp., infection with *Puccinia graminis poae* and inoculation experiments ... 541-543
Poisoning, gossypol, metabolism of animals ... 192-194
Polish wheat, crosses with *vulgare* species ... 1019-1031
Polyneuritis in pigeons, cause, feeding tests ... 464-469
Polysaccharides in sweet corn ... 427-431
Pomeroy, C. S.: Bud Selection as Related to Quality of Crop in the Washington Navel Orange ... 521-536
Poncirus trifoliata, susceptibility to citrus canker ... 227, 230
Porcupines, injury to young trees, western yellow pine and Douglas fir ... 1143, 1145
Pore, formation in aecidiospores of *Puccinia podophylli* ... 925
Pork, Ascaris-infected hogs, experiments in sensitization ... 579
Posey, G. B., and Ford, E. R.: Survey of Blister Rust Infection on Pines at Kittery Point, Me., etc ... 1253-1258
Potassium—
di-hydrogen phosphate, effect on wheat growth ... 387-390
effect on orange tree growth and composition ... 278, 281, 283
Potato beetle, insecticides ... 398, 400
Poteriostomum spp., parasite of Equidae ... 666, 667
Poultry—
consumption per capita, comparison with other meats ... 461
flesh, vitamin content ... 461-472
Powder-post beetle, temperature fatal to, determination ... 1033-1038
Powick, Wilmer C., and Hoagland, Ralph: The Chemical Composition of Edible Viscera from Meat-Producing Animals ... 339-346
Promycelia, orange rust on blackberries ... 1047-1050
Protein, decomposition by *Bacillus larvae* ... 155-157
Puccinia—
graminis—
asena, races, resistance of oat varieties ... 705-720
in the United States ... 541-548
varieties, comparisons and hosts ... 543-547
podophylli—
aecidiospores, description, and expulsion method ... 923-926
mayapple rust, expulsion of aecidiospores ... 923-926
spp., rusts of rye and barley, aecial stages ... 1119-1126
Quercetin—
a flavonol pigment in apple peel ... 1243, 1245
from apple peel, isolation and identification ... 1243-1245
Rabbitbrush, indicator of land value ... 109, 117, 118, 120-126
Rabbits, feeding with gossypol, experiments 191-196
Rainfall—
effect on spread of bean disease ... 493-495
relation to—
curly-top ... 302
strawberry leather rot ... 367-371

Page

Rands, R. D.: Snails as Predisposing Agents of Sugar Cane "Root Disease" in Louisiana ... 969-970
Ransom, B. H.: Ascaris Sensitization ... 577-582
Rations—
steer, winter and summer, composition and amount ... 1217-1218
succulent, comparison with dry rations for steers ... 1231
winter, of steers, effects on pasture gains 1215-1232
Rats—
feeding—
experiments with cottonseed kernels or gossypol ... 174-186
with gossypol, experiments ... 176-186
growth on feed containing gossypol ... 179-185
Reddy, C. S., Godkin, James, and Johnson, A. G., Bacterial Blight of Rye ... 1039-1040
Reed, H. S., and Haas, A. R. C.: Some Relations Between the Growth and Composition of Young Orange Trees and the Concentration of the Nutrient Solution ... 277-284
Reforestation activities, relation to environmental conditions ... 845, 846, 895
Reproduction, forest—
after logging in northern Idaho, factors affecting ... 1149-1157
injury by grazing and other causes ... 1145-1146
Rhagoletis pomonella—
larval development ... 1-21
metamorphosis ... 21-30, 32
See also Apple maggot; Maggot, apple.
Rhizoctonia brown rot of strawberries, description, and inoculation of fruit ... 643-645, 647, 648
Rhizopertha dominica, control in chick-peas ... 649, 658
Rhizopus nigricans, presence in cottonseed ... 286
Ribes spp.—
eradication, effect on pine infection by blister rust, survey ... 1253-1258
spread of blister rust to pines ... 1253-1255, 1257
Rice weevil, resistance to high and low temperatures ... 1043
Roberts, John W., and Dunegan, John C.: The Fungus Causing the Common Brown Rot of Fruits in America ... 955-960
Rogues, pea, crosses, results ... 1247-1252
Root disease, sugar cane, relation to snails ... 969-970
Roots, young orange trees, composition ... 282, 283
Rose, Dean H.: Leather Rot of Strawberries ... 357-376
Rot—
blue mold, citrus fruits, prevention, results of borax treatment ... 961, 968
brown—
history of fungus in Europe and America ... 955-960
of fruits in America, fungus causing ... 955-960
leather—
strawberry ... 357-376
strawberry, range and relation to rainfall ... 366-371
onion bulb, cause, and relation to environment ... 683-694
Rots—
brown, of strawberries ... 643-648
Phytophthora, literature ... 374-375
strawberry—
fruit ... 643-648
percentage of leather rot to other ... 371-372
Rubus spp., infection with orange rusts ... 1045-1058
Rust—
blister, infection of pines at Kittery Point, Me., and *Ribes* eradication ... 1253-1258
grass, inoculation experiments ... 541-543
mallow, characteristics ... 1045, 1053
mayapple, *Puccinia podophylli*, expulsion of aecidiospores ... 923-926
orange—
on blackberry, uninucleated aecidiospores ... 1045-1058
short-cycled, promycelia, characteristic features ... 1049-105
stem, resistance of oat varieties ... 705-720
Rusts—
cereal—
literature ... 718-719
literature relating to ... 547-548
physiological races, investigations and discoveries ... 705
grain, literature ... 1126

Page

Rusts—Continued.
leaf, of rye and barley, aecial stages ... 1119-1126
orange, blackberry infection ... 1045-1058
Rye—
bacterial blight ... 1039-1040
brittle straw and other abnormalities ... 169-172
cell thickness ... 173
culms, normal and brittle, analysis ... 170
inbred strains, abnormalities ... 169
leaf rust, *Puccinia dispersa*, aecial stages 1119-1126
wild, giant, indicator of land value ... 107, 120, 124
Sacaton, indicator of land value ... 106, 118, 119, 124, 125
Sage varieties, indicators of land value ... 100-113, 117-126
Sagebrush, indicator of land value 101, 108, 117-126
Salt content of cotton fiber ... 293-295
Salt bush, narrowleaf, association on Southwestern desert soils ... 759-761, 796-799
Saltgrass, association on southwestern desert soils ... 761-763, 796-799, 800
Salts, wheat nutrition ... 387-393
Samphire, indicator of land value ... 111, 118, 121, 122, 125, 126
Sando, Charles E.: The Isolation and Identification of Quercetin from Apple Peels ... 1243-1245
Sap—
cell, density, relation to environmental conditions in the Wasatch Mountains, Utah ... 845-907
concentration—
relation to osmotic phenomena ... 846-847
seasonal variations ... 888-892
density—
determination, technique ... 849-851
of plants in Wasatch Mountains ... 860-884
orange leaf, concentration and reaction, relative constancy ... 277
Satsuma oranges—
susceptibility to—
citrus canker ... 229-230
citrus scab ... 248
Sausage tree, African, host of *Heterodera radicicola* ... 1061
Sax, Karl, and Gaines, E. F.: A Genetic and Cytological Study of Certain Hybrids of Wheat Species ... 1017-1032
Scab—
citrus—
epidemic in Alabama, conditions essential for ... 249, 253
relation to environmental factors ... 241-254
yearly prevalence, conditions determining ... 249-250
pecan—
and sources of early spring infections ... 321-330
description, on leaves, nuts, twigs, catkins, and buds ... 322-324
infection source and control measures ... 324-328
Schwartze, Erich W., and Alsberg, Carl L.: Pharmacology of Gossypol ... 191-196
Relation Between Toxicity of Cottonseed and its Gossypol Content ... 173-189
Sclerotinia—
cinera, fungus causing brown rot of fruits in America ... 955-960
fructicola, same as *Sclerotinia cinerea* ... 959
spp., measurements of asci and ascospores ... 957
Scofield, C. S., and Kearney, Thomas H.: The Salt Content of Cotton Fiber ... 293-295
Seed—
coat, permeability gradient to iodin ... 225-226
coats, wheat, means of protection of embryo from hot-water injury ... 86-89
cotton—
comparisons ... 960-962
germination ... 285-292
soaking—
effects, general ... 489-490
literature referring to ... 496-497
western white pine, fall sowing and delayed germination ... 1127-1131
Seedlings—
Douglas fir, survival under different cutting systems ... 1234-1235
orange, growth and composition, effect of concentration of nutrient solution ... 278-279
Seeds—
composites, infestation with *Tylenchus dipsaci* ... 473-478

Page

Seeds—Continued.
cotton, prewetting method of germination 287–288
live, in cottonseed sample, demonstration.. 287
Seepweed—
indicator of land value... 111, 118, 121, 122, 125, 126
on southwestern desert soils..... 773, 778, 796–799
Semiarid United States, vegetation, types and their significance..... 99–128
Serological tests, cattle, for infectious abortion..... 613, 614, 617–620
Severinia buxifolia, resistance to citrus canker.. 228
Sewell, M. C.: Relation of the Molecular Proportions in the Nutrient Solution to the Growth of Wheat..... 287–303
Sex—
determination in chickens during embryonic development..... 214–220
hemp, influence of environment..... 1067–1080
ratio, chickens, experimental study and discussion..... 200–220
Shadscale, indicator of land value..... 109, 110, 118, 120, 125
Shamel, A. D.: Bud Selection as Related to Quality of Crop in the Washington Navel Orange..... 521–526
Shantz, H. L., and—
Aldous, A. E.: Types of Vegetation in the Semiarid Portion of the United States, etc..... 99–128
Piemeisel, R. L.: Indicator Significance of the Natural Vegetation of the Southwestern Desert Region..... 721–802
Sharkey clay soil, colloids from, breaking strength..... 508–512
Shaw, R. H., and Wright, P. A.: A Study of Ensiling a Mixture of Sudan Grass with a Legume..... 255–259
Shear, C. L.: Botryosphaeria and Physalospora on Currant and Apple..... 585–598
Shedd, O. M.: The Determination of Nitrate and Ammonia in Nitrogenous Materials.. 527–539
Sheep, grazing, injury to young coniferous trees..... 1145–1146
Sheets, E. W.: Effect of Winter Rations on Subsequent Pasture Gains of Steers... 1215–1232
Shelterwood—
cutting method, effect on reproduction.... 1234, 1235, 1239, 1241, 1242
method of cutting Douglas fir, effect on reproduction..... 1234, 1235, 1237, 1239–1242
Shinnery, indicator of land value..... 114, 118, 120, 123, 124
Shive's nutrient solution, formula..... 388
Shoots, young orange trees, composition.... 382, 383
Shrinkage, steers in transit and in dressing.. 1230–1231
Shrubs, Wasatch Mountains, freezing-point, depressions, and osmotic pressures..... 866–871, 878–879
Silage—
crops, mixture, typical combinations..... 255
Sudan-grass mixture with legume, palatability and composition..... 257–258
Silking, corn, relation to maturity..... 409–411
Silvanus cassiae, heating of bran..... 1105
Silver, James: The European Hare (*Lepus europaeus* Pallas) in North America... 1133–1137
Silophilus—
granarius. *See* Weevil, granary; Granary weevil.
oryza—
heating of grain..... 1105, 1113, 1115
See also Weevil, rice; Rice weevil.
Skin disease, result of Ascaris poisoning..... 578, 579, 580, 581
Skinner, J. J.: Greenhouse Experiments with Atmospheric Nitrogen Fertilizers and Related Compounds..... 971–976
Skull, meadow mouse, description and measurement of bones and teeth..... 992–1014
Skulls, meadow mouse, cleaning and preparing for collection..... 978
Slash disposal in cutting Douglas fir, effect on reproduction..... 1236–1241
Smalling, cotton growth disorder..... 810–811
Smut, wheat, hot-water treatment modified.. 79–98
Snails, relation to root disease of sugar cane in Louisiana..... 969–970
Snapdragon, infestation with *Heterodera radicicola*..... 1061

Page

Snodgrass, R. E.: Anatomy and Metamorphosis of the Apple Maggot, *Rhagoletis pomonella* Walsh..... 1–36
Snyder, T. E., and St. George, R. A.: Determination of Temperatures Fatal to the Powder-post Beetle, *Lyctus planicollis* Leconte, by Steaming Infested Ash and Oak Lumber in a Kiln..... 1033–1038
Sodium—
cyanid, fumigation of grain for insect pests.. 1106, 1107, 1108, 1113, 1114, 1115
effect on orange tree growth and composition.. 278, 281, 283
Soil—
colloids—
binding power, factors influencing..... 499–513
heat of wetting..... 927–935
moisture, relation to clubroot..... 549–562
particles, noncolloidal, heat of wetting.... 929–930
temperature, relation to clubroot..... 549–562
treatment for control of larkspur leafspot.... 209
Soils—
bacteria, effect of cyanamid and related compounds..... 1159–1166
colloidal material—
estimating, heat of wetting as basis..... 930–934
heat of wetting..... 928–929
desert, southwestern, composition and salts.. 723, 724–725
salinity, relation to chlorid content of cotton plants..... 696, 701
Soppeland, Lulu: *Flavobacterium suaveolens*, a New Species of Aromatic Bacillus Isolated from Dairy Wastes..... 275–276
Sowing western white pine seed, fall versus spring..... 1128–1131
Soybeans, silage, composition..... 258
Spacing, cotton, experiments in southern California..... 1081–1093
Sphaeropsis malorum, perfect stage found in currant..... 584–585
Spinach, susceptibility to curly-top..... 315
Spore, discharge, mechanics studies..... 923, 924, 926
Sporocarps of *Physalospora malorum*, size and structure, relation to host..... 586–587
Spraying, pecans for scab control..... 326–327
Sprays—
absorbed organic compounds, insecticidal value..... 399–400
inorganic nonarsenical compounds, testing as insecticides..... 396
pecan scab..... 326–327
Spring growth, citrus, relation to scab infection..... 243–253
Spruce, Engelmann, growth in Douglas fir forests..... 1237–1240
Squares, cotton, shedding, effect of crazy-top and other diseases..... 817
Squash lady beetle, insecticides..... 401
St. George, R. A., and Snyder, T. E.: Determination of Temperatures Fatal to the Powder-post Beetle, *Lyctus planicollis* Leconte, by Steaming Infested Ash and Oak Lumber in a Kiln..... 1033–1038
Stahl, C. F., and Eubanks, Carsner: Studies on Curly-top Disease of the Sugar Beet.. 297–320
Stakman, E. C., and Levine, M. N.: *Puccinia graminis poae* Eriks. and Henn. in the United States..... 541–548
Staminate hemp plants, description..... 1067
Star-of-Bethlehem, host of barley leaf rust..... 1124–1125
Steers—
gains on pasture, effects of winter rations..... 1215–1232
rations, winter and summer, composition and amount..... 1217–1218
shrinkage in transit and in dressing..... 1230–1231
Steiner, G.: On Some Plant Parasitic Nemas and Related Forms..... 1059–1066
Stellaria media, inoculation with curly-top.... 312, 313, 315
Stem rust, resistance of oat varities..... 705–720
Stenosis, cotton growth disorder..... 810–811
Sterility, wheat hybrids..... 1017–1032
Stevens, Neil E.—
and Dodge, B. O.: The *Rhizoctonia* Brown Rot and Other Fruit Rots of Strawberries..... 643–648

Page

Stevens, Neil E.—Continued.
Botryosphaeria and Physalospora on Currant and Apple ... 589-598
Physalospora malorum on currant ... 583-588
Stockton clay adobe soil, colloids from, breaking strength ... 511, 512
Storage, onion, relation of temperature to rot development ... 691-692, 693
Strawberries—
fruit rots ... 643-648
holding tests, rots developing, study of causes ... 373
infection in field with leather rot ... 365-366
inoculation with leather rot ... 364-365
shipments, by States, 1922 ... 367
varieties susceptible to leather rot ... 366
Strawberry leather rot ... 357-376
Strongylus spp., parasites of Equidae ... 666, 667, 672
Stroud method for nitrate determination ... 528-531
Sturtevant, A. P.: The Development of American Foulbrood in Relation to the Metabolism of Its Causative Organism ... 129-168
Sudan grass—
mixture—
with a legume, ensiling ... 255-269
with legume silage, composition ... 257-258
silage, composition ... 257-258
Sugar—
content, sweet corn, changes and tests ... 427, 434-435
determination, literature ... 487-488
in bee larvae, quantitative determination ... 141-150, 157-159
Sugars—
color values, comparison with glucose ... 484-485
determination, picric acid methods ... 479-488
Tail, meadow mouse, measurement ... 987
Tan brown rot of strawberries, description ... 645-646, 648
Tapke, V. F.: Effects of the Modified Hot-water Treatment on Germination, Growth, and Yield of Wheat ... 79-98
Taraxacum officinale. *See* Dandelion.
Taylor, J. W., and Leighty, C. E.: Hairy-neck Wheat Segregates from Wheat-Rye Hybrids ... 567-576
Teeth, meadow mouse, description, measurements, and variations ... 1010-1013, 1015
Teliospores, *Puccinia disperss*, germination 1120-1122
Temperature—
effect on spread of bean disease ... 493-495
fluctuations in duff and bare soil, comparisons ... 1154-1156
relation to—
citrus scab infection and development ... 243-253
curly-top ... 313
leather rot of strawberries ... 369, 371, 372-373
onion bulb rot, occurrence and distribution ... 689-691
Temperatures—
fatal to powder-post beetle, in ash and oak lumber ... 1033-1038
greenhouse, in wheat growing experiments ... 389
high and low, resistance of rice and granary weevils ... 1043-1044
Tecosinte, chromosome number ... 673-676, 678
Tecosinte-and-corn hybrids, chromosome number ... 674-676
Tephrosia candida—
growth and blossoming, relation to length of day ... 445-460
photoperiodism ... 445-460
Tests, corn, canning quality ... 431-433
Texas, cottonseed, germination studies ... 285-292
Thersilochus conotracheli, parasite of cambium curculio ... 385
Thompson, H. E.: Brittle Straw and Other Abnormalities in Rye ... 169-172
Thumb-nail test of corn ... 435
Timber, woodland, indicator of land value ... 116, 120, 123-126
Tims, E. C., and Walker, J. C.: A Fusarium Bulb Rot of Onion and the Relation of Environment to Its Development ... 683-694
Tipsacum dactyloides, chromosome number ... 677-678
Tobacco—
grass, indicator of land value ... 105, 118, 124, 125
nitrate determination methods ... 531-533
Tom Thumb maize, crossing with Jala maize ... 1095-1102

Page

Tomato, susceptibility to curly-top ... 314
Tomosis, cotton growth disorder ... 607-609
Tongues, composition ... 345
Toole, Eben S., and Drummond, Pearl L.: The Germination of Cottonseed ... 285-292
Tracheal system—
apple maggot ... 5-7
bee larva ... 1179-1184, 1206
Trees—
hosts of cambium curculio ... 379, 385
injury by cambium curculio ... 377-386
orange—
analysis of various parts, and ash percentage ... 282, 283
ash constituents ... 283
dry matter solubility, relation to concentration of solution ... 281-282
orchard, injury by European hares ... 1136-1137
painting wounds to prevent curculio injury ... 385
protection against hares ... 1137
reserved, in cut-over areas, silvicultural practices ... 1146-1147
Wasatch Mountains, freezing-point depressions and osmotic pressures ... 861-866, 876-877
young orange, growth and composition, relation to nutrient solution ... 277-284
Trichonema spp., parasites of the Equidae ... 670-671, 672
Triodontophorus spp., parasites of the Equidae ... 666, 667
Triticum—
dicoccum dicoccoides, genetic relation to a synthetic form ... 515-520
vulgare, cross with a variety of *Triticum durum* ... 515, 519
Trunk, young orange trees, composition ... 282, 283
Tubercles, plantar, on foot of meadow mouse, variation ... 983, 1014
Tuckwiller, David: Steer-fattening experiments ... 1215
Turkeys, flesh, vitamin B content ... 463, 468, 472
Turnips, injury by clubroot ... 551
Tussock grass, indicator of land value ... 106, 119, 125, 127
Twig, pecan, scab description and source of infection ... 324
Typhoid, fowl, dissemination and control ... 75-78
Ulsch-Street method of nitrate determination, comparisons ... 527, 533-538
Uncinaria stenocephala, occurrence in foxes ... 331
Upland cotton—
chlorid content of leaf tissue, comparison with Egyptian ... 695-704
susceptibility to crazy-top ... 824, 826
varieties, comparison with Pima cotton in Arizona ... 938-954
Weed, Star-of-Bethlehem, danger near barley fields ... 1125, 1126
Weevils—
bean—
effect of fumigation ... 348-349
egg, effect of fumigation ... 350-351
fumigation ... 347-356
resistance to high and low temperatures ... 1043-1044
within bean seeds, effect of fumigation ... 351-355
Weight, meadow mice, variations ... 988-989
West Virginia, steers, fattening ... 1217-1218
Western blight. *See* Curly-top.
Wetting, heat of soil colloids ... 927-935
Wheat—
cross, inheritance of pubescent nodes ... 841-844
crosses, literature relating to ... 572, 574, 575-576
emmer species, crosses with *vulgare* species ... 1018-1031
fertilizer experiments ... 972-975
genetics, literature ... 1031, 1032
germination, effect of modified hot-water treatment ... 80-89
groups, classification and characteristics ... 1017
growth—
and yield of modified hot-water treatment ... 89-95
relation to salts in nutrient solution ... 387-393
"hairy neck," segregates from wheat-rye hybrids ... 567-576
heating caused by insects ... 1103-1104, 1105, 1107-1109, 1113-1115

Page

Wheat—Continued.
hot-water treatment, modified, effect on germination, growth, and yield 79–98
hybrids—
sterility, causes 1017–1032
study, genetic and cytological 1017–1032
salt nutrition 387–393
seed coats, permeability to iodin 225–226
species hybrids, characters association 1025–1027
treatment literature 97
vulgare species, crosses with emmer species 1018–1031
yield, effects of modified hot-water treatment 90–95
Wheatgrass, indicator of land value 100, 102, 103, 117, 120, 124
Wheat-rye hybrids—
hairy neck segregates 567–576
self sterility 567–568, 573–575
Wilcox, Marguerite S.: *Botryosphaeria* and *Physalospora* on Currant and Apple 585–598
Willaman, J. J., and Davison, F. R.: Some Modifications of the Picric Acid Method for Sugars 479–488
Willow, indicator of land value 114, 118, 119, 123, 124, 125, 126
Wilt, bean, causes and spread 490–493
Windfall, losses caused to western yellow pine and Douglas fir 1143–1145
Winds, storm, spread of blister rust to pines 1253–1255, 1257
Wineland, Grace O.: An Ascigerous Stage and Synonomy for *Fusarium moniliforme* 909–922
Winter rations of steers, effects on pasture gains 1215–1232
Winter-fat, indicator of land value 110, 118, 120, 125, 126
Wisconsin, clubroot studies 549
Worms, control in foxes 334–337
Wounds, tree, infestation with cambium curculio 379–385
Wright, P. A., and Shaw, R. H.: A Study of Ensiling a Mixture of Sudan Grass With a Legume 255–259
Urea—
effect on numbers of bacteria in soil 1160, 1161, 1165, 1166
investigations and discussions 37–39
nitrification rates and decomposition in soil 43, 48–54
nitrogen, determination method 42
Urephos, fertilizer tests 973–975
Uromyces hordei, rust of wild barley and its aecial stage 1124
Utah, Wasatch Mountains, environmental conditions of trees, relation to density of cell sap 845–907
Vaccination—
cattle, to control infectious abortion 609–620
fowls, for control of typhoid 78
Vaccine, abortion, immunization of cattle 609–620
Van Volkenberg, H. L., and Hanson, Karl B.: Anthelmintic Efficiency of Carbon Tetrachlorid in the Treatment of Foxes 331–337

Page

Varnette, D. L.: Comparison of Pima Cotton with Upland Varieties in Arizona 937–964
Vegetation—
desert region, indicator significance 721–802
semiarid, in United States, types and significance 99–128
type, western United States, regions and key map 121–127
types—
agricultural possibilities 117–119
relation to character and productivity of the land 795–800
zones in mountainous regions of the West 845
Velvetnode wheat, heredity studies 841–844
Virus, curly-top, transmission methods and factors affecting 306–316
Viscera, edible, of meat-producing animals, chemical composition 339–348
Vitamin—
antineuritic, in poultry flesh and eggs 461–472
B, content of dried poultry flesh and eggs 462–472
Vliet, E. B.: Greenhouse Experiments with Atmospheric Nitrogen Fertilizers and Related Compounds 971–976
Vulgare wheat group, characters 1017
Wahlenberg, W. G.: Fall Sowing and Delayed Germination of Western White Pine Seed 1127–1131
Walker, J. C., and Tims, E. C.: A Fusarium Bulb Rot of Onion and the Relation of Environment to its Development 683–694
War gases, utilization as insecticides 399, 400
Warehouses, grain, fumigation experiments with chick-peas 650–659
Wasatch—
Mountain region, vegetation, temperature, precipitation, etc 851–860
Mountains, Utah, environmental conditions, relation to density of cell sap 845–907
Washington—
Experiment Station wheat hybrids, growing 1019
Hybrid 143, origin, and crosses with emmer 1019–1031
Wastes, dairy *Flavobacterium suaveolens*, a new species of aromatic bacillus 275–276
Water—
soak. *See* Rot, leather, strawberry.
supply, relation to sap density of leaves and roots 885–888
Weather, effect on citrus scab distribution and prevalence 250–252
Yolk, egg, weight and water content, relation to sex ratio 211–213
Yucca—
association with cactus on Southwestern desert soils 731–733, 797
indicator of land value 103, 114
Zebra—
nematode parasite, *Cylindropharynx ornata*, and others 661–672
parasites 666–672
Zinnia elegans roots infestation by *Paratylenchus nanus* 1064–1065

Page
57-954
21-902
90-126
21-127
17-119
95-800
845
41-844
06-316
39-346
61-472
62-472
71-976
1017
7-1131
683-694
899, 400
650-659
651-660
645-907
1019
19-1031
275-276
885-888
250-252
211-213
733, 797
103, 114
661-672
666-672
064-1065